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Index

Un index par sujet et auteur et une liste de toutes les publications parues en 1980 paraîtront au début de 1981 et seront distribués gratuitement à tous ceux qui reçoivent le *Journal*, ainsi qu'aux abonnés. On pourra se procurer des exemplaires supplémentaires à la Direction de l'information et des publications scientifiques.

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Digestibilité chez la Truite arc-en-ciel (*Salmo gairdneri*) lors de l'adaptation à un nouveau régime alimentaire

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DE LA NOÜE, J., G. CHOUBERT, B. PAGNIEZ, J.-M. BLANC ET P. LUQUET. 1980. Digestibilité chez la Truite arc-en-ciel (*Salmo gairdneri*) lors de l'adaptation à un nouveau régime alimentaire. Can. J. Fish. Aquat. Sci. 37: 2218–2224.

Après discussion de la méthodologie à utiliser pour l'étude de la digestibilité chez les poissons, nous avons tenté de définir quelques contraintes expérimentales nécessaires à l'obtention d'une bonne précision des coefficients d'utilisation digestive chez la Truite arc-en-ciel (*Salmo gairdneri*): temps de latence à respecter après changement de régime alimentaire, durée de récolte des fèces et nombre de répétitions. Pour ce faire, nous avons chaque jour récolté de façon automatique et analysé les fèces de cinq lots de 15 poissons pendant les 20 jours qui suivent l'administration d'un nouveau régime alimentaire. Dès le 3^e jour après le changement d'aliment, les coefficients d'utilisation digestive prennent des valeurs définitives caractéristiques de ce régime; il n'existe donc pas de phénomènes d'adaptation, seul est noté un temps de latence lié à la vitesse de transit digestif. On peut dès lors procéder à la collecte des fèces dès le 3^e jour après un changement de régime alimentaire. Enfin on a établi, *a posteriori*, des combinaisons « nombre de répétitions × nombre de jours » à employer pour une précision donnée des résultats de coefficient d'utilisation digestive.

Mots clés: truite arc-en-ciel, coefficient d'utilisation digestive, temps d'adaptation, nombre de répétitions

DE LA NOÜE, J., G. CHOUBERT, B. PAGNIEZ, J.-M. BLANC ET P. LUQUET. 1980. Digestibilité chez la Truite arc-en-ciel (*Salmo gairdneri*) lors de l'adaptation à un nouveau régime alimentaire. Can. J. Fish. Aquat. Sci. 37: 2218–2224.

We have investigated the experimental conditions necessary to obtain accurate digestibility coefficients in rainbow trout (*Salmo gairdneri*). These conditions concern the lag period which should be observed after changing the diet, the duration of feces collection, and the number of replicates. Every day we collected automatically and then analyzed the feces of five groups of 15 fish each during the 20 d following the administration of a new diet. As early as the 3rd d after changing the diet, digestibility coefficients took definitive values characteristic of that diet. Thus, there were no adaptation phenomena; we observed only a lag period associated with digestive transit rate. Feces may be collected as soon as on the 3rd d after changing the diet. Finally, "number of replicates × number of days" combinations were established to obtain a given accuracy of digestibility coefficients.

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LA digestibilité d'une matière première ou d'un aliment représente la quantité absorbée rapportée à la quantité ingérée; elle s'estime par différence en mesurant la fraction éliminée dans les fèces. La récolte de ces dernières, en vue de la détermination des coefficients d'utilisation digestive chez le poisson, se heurte à des problèmes spécifiques aux animaux aquatiques: récolte quantitative, phénomènes de dissolution.

Ceci explique que la méthode directe, consistant à mesurer la totalité de l'ingéré et de l'excrété, mise en oeuvre par Tunison et al. (1948), ait été peu utilisée. Seuls Smith (1971, 1976), utilisant la chambre à métabolisme de Post et al. (1965) et Ogino et al. (1973) l'ont pratiquée.

Aussi, la méthode indirecte, qui ne nécessite pas la récolte quantitative des excréments est-elle couramment utilisée. Encore convient-il que l'échantillon de fèces prélevé soit effectivement représentatif et en premier lieu que leur composition soit la plus proche possible de celle qu'elles avaient lors de leur émission. En conséquence, les techniques basées sur le siphonnage des fèces au fond des bacs semblent à proscrire compte tenu des phénomènes de dissolution (Inaba et al. 1962; Possompès 1973; Cho et Slinger 1979; Windell et al. 1978). En effet, les phénomènes de dissolution interviennent dès les 5 premières minutes d'immersion (Possompès

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1973), entraînant au bout d'une heure une surestimation du coefficient d'utilisation digestive de 10% pour la matière sèche et les protéines (Windell et al. 1978).

Ceci explique la faveur qu'ont les techniques consistant à prélever directement au niveau du gros intestin une fraction du contenu digestif qu'on assimile ainsi à des fèces. Cette collecte est effectuée soit par massage abdominal (Inaba et al. 1962; Nose 1967; Possompès 1973), soit par dissection (Phillips et al. 1948; Nose 1960; Hirao et al. 1960; Kitamikado et al. 1964; Austreng 1978), soit par succion anale (Windell et al. 1978) ou grâce à l'introduction d'un cathéter dans l'anus (Smith et Lovell 1971). Ces techniques sont simples à mettre en oeuvre mais encore sujettes à critique, car les échantillons ainsi recueillis ne sont que des contenus digestifs et non réellement des fèces. Les observations de Smith et Lovell (1971), d'Austreng (1978) et de Windell et al. (1978) laissent penser qu'il existerait une absorption au niveau du gros intestin; de même, les observations microscopiques effectuées par Gas (1976) chez la Carpe (*Cyprinus carpio*) et par Bergot (1976) chez la Truite arc-en-ciel (*Salmo gairdneri*), indiquent qu'une absorption de macromolécules protéiques aurait lieu au niveau de l'intestin postérieur. On peut, d'autre part, reprocher à ces techniques de ne prélever que des échantillons ponctuels non représentatifs de l'ensemble des fèces pendant tout un nycthémère. Or, Possompès (1973) et Furukawa (1973) ont montré qu'il existe des variations dans la composition des fèces au cours de la journée.

Un prélèvement en continu tout au long du nycthémère des fèces émises naturellement par le poisson, mais avec un temps d'immersion très court (quelques dizaines de secondes au maximum), est donc préférable; c'est ce que nous nous sommes efforcés de réaliser en mettant en oeuvre une méthode de collecte en continu des excréments (Kaushik et Luquet 1976; Choubert et al. 1979). Le dernier appareillage décrit, d'ailleurs en cours d'amélioration, présente en outre un caractère quantitatif.

D'autres points méthodologiques restent cependant encore à préciser. Ainsi, le temps d'adaptation des poissons à leurs nouvelles conditions alimentaires varie selon les auteurs de 3 jours pour la Carpe *Cyprinus carpio* (Kim 1974) ou la Truite arc-en-ciel *Salmo gairdneri* (Smith 1971) à 15 jours pour la Truite arc-en-ciel *Salmo gairdneri* (Singh et Nose 1967; Windell et al. 1978; Kaushik et Luquet 1976). De même, le temps durant lequel la récolte des fèces est effectuée varie de 1 jour (Phillips et al. 1948; Nose 1960; Hirao et al. 1960; Kitamikado et al. 1964; Smith et Lovell 1971; Austreng 1978; Windell et al. 1978) à 15 jours (Kaushik et Luquet 1976).

Le présent travail a donc pour objet de mieux préciser les conditions expérimentales à employer lors de mesures de routine de la digestibilité chez la Truite arc-en-ciel. En valorisant les avantages de l'appareil de récolte précédemment décrit (Choubert et al. 1979), nous avons étudié le temps durant lequel il est nécessaire d'adapter les poissons à de nouvelles conditions alimentaires, le nombre de répétitions et la durée de récolte à respecter afin d'obtenir une bonne précision du coefficient d'utilisation digestive.

TABLEAU 1. Composition des régimes alimentaires (matière sèche).

Composant	Aliment témoin	Aliment expérimental
Composition centésimale		
Farine de Hareng du Danemark	96	25
Blé entier broyé		32
Tourteau de soja		15,8
Gluten de maïs		8
Tourteau de colza		6
Farine de sang		5
Huile de poisson		3
Lignosulfite de calcium		2
Complément vitaminique[a]	2	2
Complément minéral[b]	2	1
Concentré de canthaxanthine[c]		0,2
Oxyde de chrome	1	0,5
Caractéristiques analytiques		
Protéines brutes (N × 6,25)	71,23	43,85
Cendres (%)	18,5	8,26
Amidon (%)	—	23,68
Canthaxanthine (μg/g)	—	215
Énergie (J g^{-1})	21 476,84	21 000,32

[a] European Inland Fisheries Advisory Commission (1971).

[b] Luquet (1971).

[c] Carophyll, Rouge, F. Hoffmann-Laroche, 52 blvd. du Parc — 92 Neuilly-sur-Seine, France.

Matériel et méthodes

Après changement du régime alimentaire distribué aux poissons, on suit journellement l'évolution des coefficients d'utilisation digestive. L'expérience a été réalisée sur des truites arc-en-ciel (*Salmo gairdneri*) d'un poids moyen initial de 160 g, réparties au hasard en cinq lots de 15 individus, placés dans des bacs cylindroconiques de 40 cm de diamètre et d'une capacité utile de 50 L. Chaque bac est alimenté en eau selon un débit de 4 L min^{-1} et une température maintenue à 14 ± 1°C. Les bacs expérimentaux sont installés sous abri et reçoivent 12 h par jour un éclairage artificiel (4800 lumens/m^2) assuré par des tubes fluorescents.

Les truites sont nourries deux fois par jour à 09:00 et 16:30, 7 jours par semaine. L'aliment est distribué à chaque repas suivant la méthode décrite par Luquet (1971). Pendant la période d'adaptation au bac, soit pendant un mois, les poissons reçoivent, à satiété, un aliment témoin dont la composition est donnée dans le tableau 1. Pendant l'expérience proprement dite d'une durée de 20 jours (printemps 1978), un aliment « expérimental » dont la composition est donnée dans le tableau 1 est distribué aux poissons. Le pressage des aliments se fait sans adjonction d'eau (presse de laboratoire CPM). Les granulés fabriqués ont un diamètre de 2,5 mm et une longueur d'environ 4 mm. Les aliments sont conservés et stockés en chambre froide

(+4°C) jusqu'à leur utilisation. Les relevés des quantités d'aliment ingéré sont effectués chaque jour à chaque repas pour chaque bac.

La récolte des fèces s'effectue à l'aide du dispositif précédemment décrit (Choubert et al. 1979), dont le principe est le suivant: l'eau d'évacuation des aquariums qui contiennent les poissons passe à travers des grilles métalliques qui retiennent les fèces, les séparent de l'eau et, par un mouvement de rotation, les soustraient du lessivage et les projettent sur des plateaux où elles sont immédiatement congelées. Chaque jour les plateaux contenant les fèces sont changés et leur contenu est lyophilisé, broyé, pesé et conservé en contenants hermétiques jusqu'aux analyses.

MÉTHODES ANALYTIQUES ET STATISTIQUES

Les coefficients d'utilisation digestive apparente (CUDa) de l'azote total, de l'amidon et de l'énergie sont calculés sur les échantillons de fèces obtenus chaque jour. Les coefficients d'utilisation digestive de la canthaxanthine, pigment caroténoïde de synthèse, ne sont calculés que tous les deux jours compte tenu de l'importance de la prise d'essai nécessaire pour le dosage. La relation formulée par Maynard et Loosli (1969) sert de base au calcul du CUDa.

Le dosage de l'azote total est effectué selon la méthode de Kjeldahl sur des prises d'essai de 400 mg pour l'aliment et 50 mg pour les fèces; l'amidon selon la méthode de Dubois et al. (1956) sur une prise d'essai de 100 mg d'aliment sec ou de fèces; la canthaxanthine selon la méthode décrite par Osadca et al. (1972) sur une prise d'essai de 15 g d'aliment sec ou 1 g de fèces; la valeur de l'énergie des aliments et des fèces à l'aide d'une bombe calorimétrique adiabatique Gallenkampf sur 1,5 g d'aliment sec ou de fèces; la matière sèche des aliments par chauffage à 95°C pendant 24 h sur une prise d'essai de 2 g; l'oxyde de chrome selon la méthode de Bolin et al. (1952) sur une prise d'essai de 100 mg d'aliment sec ou de fèces pour servir de base aux calculs de digestibilité. Chaque dosage est exécuté en double.

L'exploitation statistique des résultats a été effectuée selon un modèle factoriel à effets aléatoires (bacs, jours) supposant l'absence d'interaction. Nous avons donc utilisé la méthode classique d'analyse de la variance décrite par Snedecor et Cochran (1967); les calculs d'erreur sur les composantes de variance ont été établies d'après Becker (1967).

Résultats

Les quantités de fèces récoltées sont en moyenne de 3,95 ± 1,48 g poids sec par bac et par jour.

La figure 1 rapporte les variations de la concentration quotidienne de l'oxyde de chrome, de l'azote, de l'énergie, de l'amidon et de la canthaxanthine dans les fèces. La diminution des concentrations en oxyde de chrome observée pour les jours 1 et 2 est très nette et dépend, en partie, de la teneur en oxyde de chrome plus faible de l'aliment expérimental. À partir du jour 3, la teneur en oxyde de chrome des fèces oscille de façon non significative autour d'une valeur moyenne (1,28 ± 0,07%). L'évolution de la concentration de l'azote total est sensiblement identique à celle de l'oxyde de chrome. À partir du 3e jour, les teneurs en azote total des fèces oscillent de façon non significative autour d'une valeur moyenne (1,85 ± 0,04%). Le comportement des teneurs en amidon, canthaxanthine et des valeurs énergétiques est différent. Il y a augmentation des concentrations durant les jours 1 et 2 et stabilisation à partir du jour 3.

TABLEAU 2. Statistiques des CUDa journaliers (CUDa moyens des 5 bacs).

Période[a]	Matière sèche	Azote	Énergie	Amidon	Canthaxanthine
jours 1 à 20					
n	20	20	20	20	10
M	62,20	89,37	71,59	28,50	66,29
S	6,47	0,91	5,82	17,54	11,37
test jour 1	$P<0{,}001$	$P<0{,}01$	$P<0{,}001$	$P<0{,}001$	$P<0{,}01$
jours 2 à 20					
n	19	19	19	19	pas de mesure au jour 2
M	60,97	89,24	70,44	25,09	
S	3,47	0,71	2,86	8,55	
test jour 2	$P<0{,}005$	$P<0{,}025$	$P<0{,}001$	$P<0{,}005$	
jours 3 à 20					
n	18	18	18	18	9
M	60,36	89,15	69,91	23,55	62.86
S	2,29	0,61	1,72	5,95	3,95
test jour 3	$P>0{,}5$	$P>0{,}5$	$P>0{,}5$	$P>0{,}5$	$P>0{,}5$
I.C. (95%)	55,5–65,2	87,9–90,4	66,3–73,5	11,0–36,1	53,8–72,0
h	0	0	0	0	0

[a] *n*: Nombre de mesures (moyennes des 5 bacs) dans la période considérée: *M*: Moyenne de ces mesures; *S*: Ecart-type de ces mesures; test jour 1, 2, 3; Seuil de probabilité de l'écart par rapport à *M*; I.C. (95%): Intervalle de confiance des *n* mesures (jours 3 à 20); h: Nombre de mesures se situant hors de l'intervalle de confiance.

La figure 2 illustre l'évolution temporelle des coefficients d'utilisation digestive apparente de la matière sèche de l'azote, de l'amidon, de l'énergie et de la canthaxanthine de l'aliment expérimental.

Le CUDa de l'azote montre une constance remarquable à partir du jour 3. Pour la matière sèche et l'énergie, on observe également une stabilisation des CUDa à partir du jour 3, avec, par la suite, de faibles oscillations autour d'une valeur moyenne qui se maintient jusqu'au jour 20. Le parallélisme des courbes représentatives de l'évolution de ces CUDa illustre l'excellente corrélation ($r = 0{,}95$) qui existe entre ces deux paramètres. Si l'on porte le CUDa de la matière sèche en abscisse et celui de l'énergie des fèces en ordonnée, la relation trouvée est $Y = 257{,}26 \pm 0{,}73\ X$, pour la période jour 3 à jour 20.

Dans le cas de l'amidon, l'évolution est moins régulière. Après une chute considérable durant les 5 premiers jours, on note un pic au 9e jour suivi d'une nouvelle chute jusqu'au jour 19. Malgré cette variabilité, la corrélation entre l'amidon et l'énergie dans les fèces reste bonne ($r = 0{,}88$).

L'évolution temporelle du CUDa de la canthaxanthine est très irrégulière. La chute de 3 jours s'explique par le fait que l'aliment témoin ne contient pas de canthaxanthine. Par la suite, le CUDa oscille autour d'une valeur moyenne de l'ordre de 60%.

Dans le tableau 2 sont rapportées les statistiques des CUDa journaliers pour les périodes concernant les jours 1 à 20, 2 à 20 et 3 à 20 de la matière sèche, de l'azote, de l'énergie, de l'amidon et de la canthaxan-

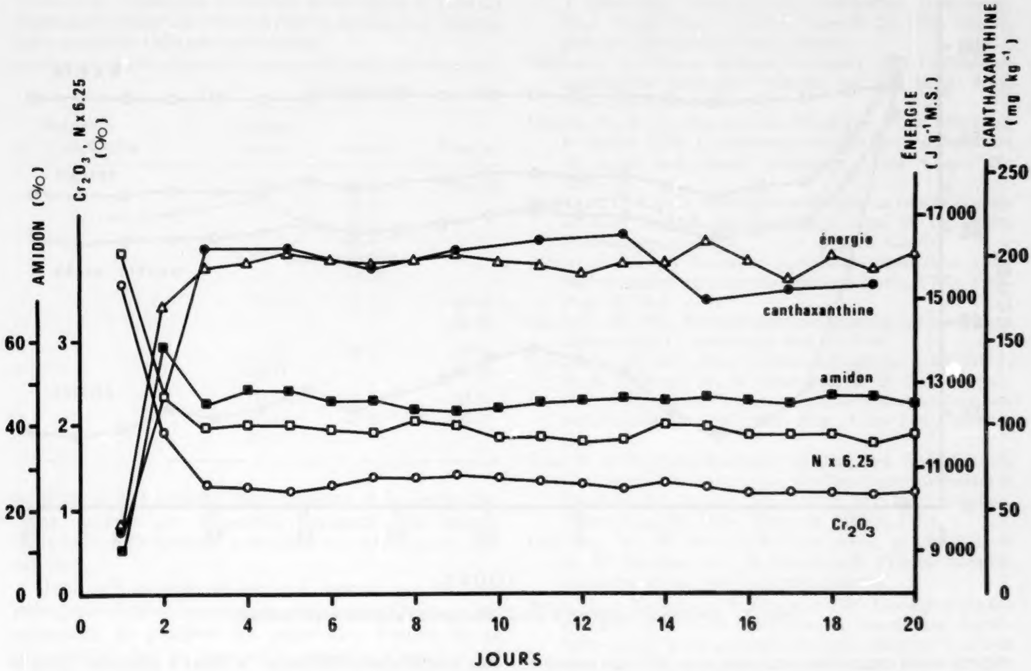

FIG. 1. Changements temporels de la composition des fèces.

thine. Ces statistiques confirment, dans tous les cas, l'hétérogénéité des mesures des jours 1 et 2 par rapport aux mesures ultérieures.

La décomposition de la variance en fonction des différentes sources de variation dont on peut estimer les effets (bacs, jours et erreur résiduelle) a été effectuée à partir des analyses des jours 3 à 20. Les résultats sont présentés dans le tableau 3 avec les écarts-types d'erreur correspondants. Ceux-ci ne permettent pas de déterminer des intervalles de confiance, la distribution d'une variance n'étant pas symétrique (Snedecor et Cochran 1967), mais ils donnent une idée de l'imprécision des résultats due à un échantillonnage limité en jours et en bacs. On observe néanmoins que la contribution de « l'effet bac » à la variation totale est généralement faible. La contribution « jour » est plus importante et représente environ 45% de la variance totale par la matière sèche, l'amidon et l'énergie. Cette composante « jour » est nulle pour la canthaxanthine qui montre une situation inverse.

Discussion et conclusions

Après changement du régime alimentaire, le temps de latence observé est dû plus probablement à la vitesse de transit qu'à une adaptation physiologique ou biochimique (changement de structure ou inductions enzymatiques par exemple). En effet, les compositions des régimes alimentaires distribués au cours de cette expérience avaient été établies afin de mettre en évidence un tel temps d'adaptation. Ainsi, le régime témoin constitué exclusivement de farine de poisson doit être considéré comme un régime « facile » sur le plan digestif, car il ne renferme qu'une matière première présentant classiquement une bonne utilisation digestive tant des protéines que de l'énergie (Nose 1967; Possompès 1973); les CUDa correspondants sont respectivement de 91 et de 92% dans le cas présent. Inversement, le

TABLEAU 3. Estimation des composantes de la variance des CUDa de l'aliment expérimental, jours 3 à 20. (Les écarts-types approximatifs des estimateurs sont indiqués entre parenthèses.)

Sources de variation	Matière sèche	Azote	Énergie	Amidon	Canthaxanthine
Bacs	0,9 (0,7)	0 (0,01)	1,0 (0,7)	6,4 (4,8)	59,8 (39,9)
Jour	4,4 (1,7)	0,2 (0,1)	2,5 (1,0)	28,6 (11,5)	0 (6,8)
Erreur résiduelle	4,0 (0,7)	0,7 (0,1)	2,1 (0,4)	33,8 (5,7)	81,8 (19,9)

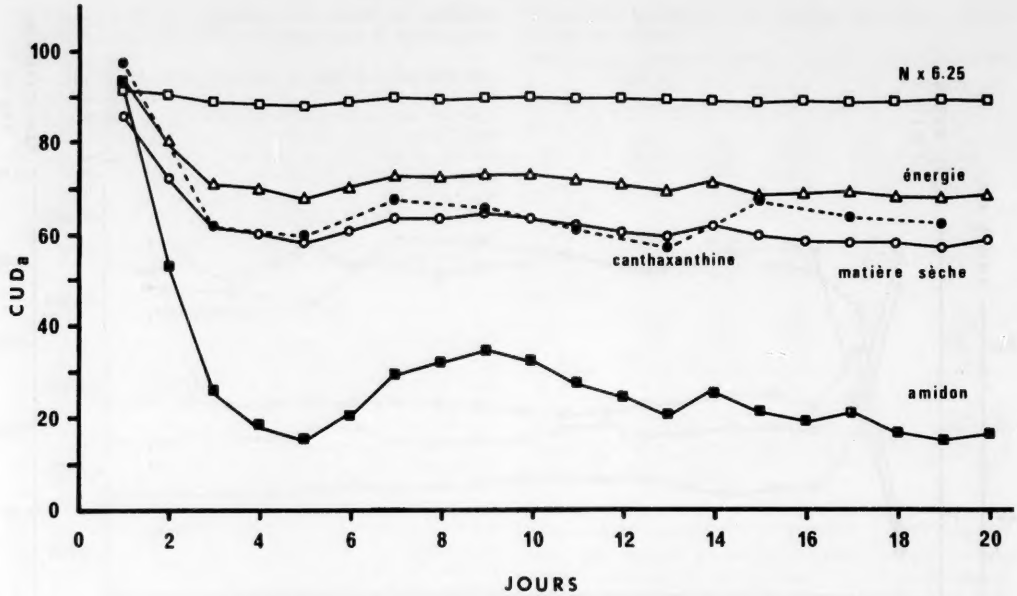

FIG. 2. Évolution temporelle des CUDa pour l'aliment expérimental.

régime expérimental ne renferme que 30% de matières premières d'origine animale, mais plus de 60% de produits végétaux ayant une moins bonne utilisation digestive tant pour les protéines que pour l'énergie (Hastings 1969). En particulier, le régime expérimental renferme 24% d'amidon dont on connaît la mauvaise utilisation digestive chez les salmonidés (Phillips et al. 1948; Inaba et al. 1973; Singh et Nose 1967; Smith 1971). Or, nous constatons que dès le 3e jour, le CUDa des différents composants alimentaires est stabilisé malgré le caractère « difficile » sur le plan digestif du régime expérimental utilisé. Ceci confère donc à des résultats une dimension plus générale.

La variation des valeurs des coefficients d'utilisation digestive pendant les 2 premiers jours de prélèvement s'explique par le mélange, dans le tractus digestif et par conséquent dans les excréments, de l'aliment antécédent et de l'aliment expérimental. À la température d'acclimatation retenue pour nos conditions expérimentales, le seul temps de vidange gastrique est de 36 h (Windell et Norris 1969). Les valeurs moyennes quotidiennes des coefficients d'utilisation digestive des principes alimentaires atteignent une relative stabilité dès le 3e jour après le changement de régime.

On peut dès lors en conclure que, dans nos conditions expérimentales, il est possible de procéder à la collecte des fèces dès le 3e jour après un changement de régime alimentaire.

Cependant lorsqu'il sera procédé à des mesures d'estimation des coefficients d'utilisation digestive à une température différente, le délai à observer après le changement de régime alimentaire sera à modifier, compte tenu de l'effet de la température sur le temps de rétention des aliments dans le tube digestif (Shrable et al. 1969; Brett et Higgs 1970; Tyler 1970; Edwards 1971; Elliot 1972; Possompès et al. 1975).

Bien que très imprécises, nos estimations des composantes de la variance des CUDa permettent d'apprécier les fluctuations susceptibles d'affecter les phénomènes digestifs dans le temps et d'un lot expérimental à un autre. À la relative stabilité des CUDa de la matière sèche de l'azote et de l'énergie s'oppose la variabilité des CUDa de l'amidon et de la canthaxanthine. Les fluctuations dans le temps présentent un caractère assez général et mériteraient une analyse plus approfondie de leurs causes réelles en fonction, notamment, du mode de nourrissage. De plus des différences entre bacs, peuvent refléter, en partie, une hétérogénéité de matériel biologique qu'il conviendrait de vérifier.

Enfin, à partir des composantes de la variance d'un CUDa il est possible de calculer la précision probable que l'on obtiendrait sur la moyenne générale pour un nombre de bacs et un nombre de mesures journalières après le temps de latence donné. Par suite, on peut estimer approximativement les nombres de bacs ou de jours à prévoir au minimum, dans une expérience semblable à la nôtre, en vue d'une précision souhaitée *a priori*. Le tableau 4 donne, à titre indicatif, les plans expérimentaux ainsi requis pour la matière sèche, l'azote et l'énergie. Une précision comparable ($<5\%$)

TABLEAU 4. Estimation du nombre de bacs (B) et de jours (J) requis pour obtenir une précision relative donnée pour diverses composantes de l'aliment expérimental.

	Composantes		
Précision en % du CUDa	Matière sèche	Azote	Énergie
1	>5B 14J	2B 6J 3B 5J 4B 4J	>5B 14J
2	>5B 14J	2B 4J 3B 5J	>5B 14J
3	5B 14J	2B 3J	4B 8J 5B 7J
4	4B 9J 5B 7J	2B 3J	3B 7J 4B 5J
5	3B 10J 4B 6J 5B 5J	2B 3J 3B 2J	3B 5J 4B 4J

ne pourrait être obtenue pour l'amidon et la canthaxanthine, qu'avec des dispositifs beaucoup plus importants mais difficilement prévisibles compte tenu de nos résultats.

Quoi qu'il en soit, au fur et à mesure que les connaissances se développeront en ce domaine, il apparaîtra nécessaire de planifier les protocoles d'étude de la digestibilité chez les poissons en fonction d'une fiabilité suffisante de l'information à obtenir.

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Myxosoma cerebralis: Trypsinization of Plankton Centrifuge Harvests Increases Optical Clarity and Spore Concentration

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MARKIW, M. E., AND K. WOLF. 1980. *Myxosoma cerebralis*: trypsinization of plankton centrifuge harvests increases optical clarity and spore concentration. Can. J. Fish. Aquat. Sci. 37: 2225–2227.

Pepsin, pronase, and trypsin were compared for their ability to digest the tissue residues that constitute the overwhelming mass of plankton centrifuge harvests. Trypsin was preferred; a treatment with 0.25% for 30 min at pH 7.2–7.5 released an average of 22% additional spores and resulted in an average 11-fold increase in spore concentration. The procedure significantly enhances the sensitivity of spore detection by the plankton centrifuge method.

Key words: Myxosoma cerebralis, myxosporidans, spore detection

MARKIW, M. E., AND K. WOLF. 1980. *Myxosoma cerebralis*: trypsinization of plankton centrifuge harvests increases optical clarity and spore concentration. Can. J. Fish. Aquat. Sci. 37: 2225–2227.

Nous avons comparé l'apptitude de la pepsine, de la pronase et de la trypsine à digérer les résidus de tissu qui constituent la presque totalité de la masse des récoltes de plancton au centrifuge. Nous préférons la trypsine; un traitement à 0,25% pendant 30 min au pH de 7,2–7,5 met en liberté, en moyenne, 22% de spores supplémentaires et produit une augmentation de concentration des spores de 11 fois en moyenne. Cette méthode rehausse de façon significative la sensibilité de la détection des spores par la méthode de centrifugation du plancton.

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THE literature on whirling disease contains an array of procedures that have been used to release and isolate spores of the causal organism, *Myxosoma cerebralis*; however, the methods are not equally applicable for diagnosis and detection. The *Fish Health Blue Book* (McDaniel 1979) indicates that where *M. cerebralis* is thought to be causing disease, a rather simple diagnostic procedure can be used: heads of suspect fish are defleshed and ground and the resulting materials examined microscopically. Spores are typically abundant in fish with clinical whirling disease, and the speed and simplicity of the method are advantageous. In contrast, spores are typically far less numerous in asymptomatic carriers and simple diagnostic procedures are usually not sufficient for sensitive and reliable detection. For that reason, the American Fisheries Society sanctions only two procedures for spore detection — the digest method developed by Markiw and Wolf (1974) and the plankton centrifuge method described by O'Grodnick (1975).

Each procedure has its particular advantages and disadvantages. Harvest volume of the digest method is but a millilitre or less and although it consists of tissue-free spores, the time required for processing is about 8 h. Harvests of the plankton centrifuge procedure occupy many millilitres, and the yield of spores is mixed with a much greater volume of host tissue fragments. However, because the centrifuge method is simpler and requires but several hours to perform, it has found decided favor with many fish health specialists and diagnosticians. Accordingly, we sought to increase the sensitivity of spore detection of the plankton centrifuge method and to obtain spores that could be serologically identified by the fluorescent antibody technique (Markiw and Wolf 1978) with little background interference from autofluorescing tissue residues. We compared pepsin, pronase, and trypsin for their ability to reduce tissue residues and thereby increase the concentration of spores in the sample.

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Materials and Methods

PRELIMINARY TRIALS

Trout infected with whirling disease were dispatched, held at 50°C for 5–10 min, and defleshed, and their skeletal elements blended then processed with a plankton centrifuge. Resulting spore populations were quantified by microscopic count; the material was then digested for 30 min with pepsin, trypsin, or pronase, and spores were again concentrated by centrifugation and quantified. Pepsin was used at a concentration of 0.5%, at pH 1.8–2.0 and 37°C. Trypsin and pronase were each used at several concentrations in the range of 0.05–0.25%, at pH 7.2–7.5 and 8.0–8.5 and 24 ± 2°C.

TABLE 1. Effects of trypsinization in releasing and concentrating *Myxosoma cerebralis* spores obtained by the plankton centrifuge method.

Material	Volume (mL)	Volume of aqueous suspension (mL)	Spore count		Effective concentration of spores[a]
			No. per mL	Total	
Plankton centrifuge residues (60 fingerlings)	13	150	20 420	3 063 000	—
Trypsinization pellet	2.5	20	202 500	4 050 000	10-fold
Plankton centrifuge residues (60 yearlings)	12	648	50 000	32 400 000	—
Trypsinization pellet	3	60	608 540	36 512 400	12-fold

[a]Derivation: $$\frac{\text{Spores per mL of resuspended digestion pellet}}{\text{Spores per mL of plankton centrifuge residues}}.$$

DEFINITIVE TRIALS

Two trials were conducted, each with 60 intact heads (neither heated nor defleshed) of brook trout (*Salvelinus fontinalis*) — one group from fingerlings and the other from yearlings. Plankton centrifuge harvests from each trial were pooled and resuspended in 100 or more volumes of water, the spores were quantified, and the harvests treated with 10–20 volumes of 0.25% trypsin in Rinaldini's solution[1] at pH 7.2–7.5 for 30 min at room temperature. Digestion was stopped by adding an aqueous solution of bovine serum albumin to a final concentration of 1%. The mixture was centrifuged at 1200 × *g* for 10 min, the resulting pellet resuspended in 20 volumes of water — an empirically determined dilution that facilitated spore counting — and the average spore count again determined.

Results

PRELIMINARY TRIALS

The preliminary trials showed that when heated and defleshed cranial and axial skeletal elements were reduced in a blender some of the spores were physically damaged, and subsequent digestion with pepsin at 37°C for 30 min was additionally destructive. Trypsin or pronase were satisfactorily gentle in the near-physiological range of pH 7.2–7.5, but digestion with either enzyme at pH 8.0–8.5 damaged many spores. Digestion with either trypsin or pronase resulted in a loss of about half the spores, but because tissue residues were removed and the volume was reduced, there was an effective 25-fold concentration with trypsin and 29-fold concentration with pronase.

DEFINITIVE TRIALS

The use of trypsin on plankton centrifuge harvests of either fingerling or yearling trout infected with whirling disease released an average of 22% (range, 13–32%) additional spores and permitted a 10- to 12-fold concentration of spores over that in the original harvest (Table 1).

Discussion

Results from the preliminary trials and the definitive work were in general agreement; trypsin or pronase effectively digested the tissue residues that contribute the bulk of plankton centrifuge harvests and released additional spores. Spores were significantly concentrated and sensitivity of detection was increased. We are not certain why spores were lost in the preliminary trials. We speculate that the heating step used to aid in defleshing increased the vulnerability of the spores to blending and to subsequent digestion. When heating and defleshing were omitted from the definitive work, spore numbers increased 32% in the harvest from fingerlings and 13% in that from yearlings.

The American Fisheries Society's *Blue Book* specifies that, in disease situations (diagnostic procedures by the plankton centrifuge method), material to be triturated be processed in 5% formalin as a means of killing spores and thus minimizing the chance of accidental dissemination of whirling disease. However, formalin should not be used when digestions are to be done, because tissue and enzymes become chemically denatured and digestion is prevented.

We stress that tryptic digestion of plankton centrifuge harvests is not intended as a routine additional step. Trypsinization is strongly suggested as a precautionary procedure for increasing the sensitivity of detection if spores are not found in plankton centrifuge harvests. Trypsinization greatly reduces the obstruction of autofluorescing background tissue and significantly increases spore concentration.

In operating the plankton centrifuge, we have found it advantageous to make a single harvest of the materials sedimented in the cup to save the time and effort required for multiple small harvests. In addition, the sedimented material can be resuspended in reduced volumes of water and allowed to settle for 2–3 min and the supernatant liquid searched for spores.

MARKIW, M. E., AND K. WOLF. 1974. *Myxosoma cerebralis*: isolation and concentration from fish skeletal elements — sequential enzymatic digestions and purification by differential centrifugation. J. Fish. Res. Board Can. 31: 15–20.

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[1] Composition: NaCl, 8.0 g; KCl, 0.25 g; $C_6H_5O_7 \cdot 2H_2O$ (sodium citrate) 1.0 g; $NaH_2PO_4 \cdot H_2O$, 0.05 g; $NaHCO_3$, 1.0 g; glucose, 1.0 g; and water to 1000 mL (Rinaldini 1959).

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Differentiation in *Coregonus zenithicus* in Lake Superior[1]

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TODD, T. N., AND G. R. SMITH. 1980. Differentiation in *Coregonus zenithicus* in Lake Superior. Can. J. Fish. Aquat. Sci. 37: 2228–2235.

Morphological variation in *Coregonus zenithicus* has long plagued biologists working on Lake Superior ciscoes. Some of this variation is due to allometric growth; earlier workers incorrectly recognized large *C. zenithicus* as a distinct species, *C. nigripinnis cyanopterus*. *Coregonus reighardi dymondi* is a variant of *C. zenithicus* in northern bays of Lake Superior and Lake Nipigon. The morphological differences between members of spring and fall spawning populations of *C. zenithicus* in Lake Superior are no greater than those between geographically separate populations. We conclude that spawning time and geographic isolation act similarly in effecting differentiation of coregonine populations, and that populations with different spawning times do not necessarily represent different species.

Key words: Coregonus zenithicus, cisco, Great Lakes, multivariate morphometrics, endangered species, taxonomy

TODD, T. N., AND G. R. SMITH. 1980. Differentiation in *Coregonus zenithicus* in Lake Superior. Can. J. Fish. Aquat. Sci. 37: 2228–2235.

Depuis longtemps, la variation morphologique de *Coregonus zenithicus* cause des ennuis aux biologistes qui étudient les ciscos du lac Supérieur. Une partie de cette variation est due à la croissance allométrique; certains chercheurs ont jadis considéré à tort les grands *C. zenithicus* comme espèce distincte, *C. nigripinnis cyanopterus*. *Coregonus reighardi dymondi* est un mutant de *C. zenithicus* dans les baies septentrionales des lacs Supérieur et Nipigon. Les différences morphologiques entre les membres des populations de *C. zenithicus* frayant au printemps et celles frayant à l'automne dans le lac Supérieur ne sont pas plus grandes que les différences entre des populations séparées géographiquement. Nous concluons que la saison de ponte et l'isolation géographique agissent de la même façon dans la différenciation des populations de Coregoninae et que les populations frayant à différentes saisons ne représentent pas nécessairement des espèces différentes.

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THE phenotypic characteristics of Great Lakes ciscoes (*Coregonus* spp.) are highly variable and are especially susceptible to environmentally-induced modification (Hile 1937; Loch 1974), making the group's taxonomy among the most complex of North American fish groups. This considerable morphological plasticity, together with possible hybridization (Smith 1964), causes problems in identification and uncertainty about the validity of previously named forms. Some of the species are extinct while others are in danger of extinction (T. N. Todd 1978. Status report on Great Lakes coregonines. Great Lakes Fishery Laboratory, Ann Arbor, Michigan). Uncertainty about the taxonomic validity of these species, particularly those that are possibly endangered, prevents effective management and protection of them.

Application of the biological species concept (e.g. Mayr 1969) to coregonines has always been difficult. Reproductive integrity is nearly impossible to establish for most of the species that have been described from the Great Lakes. Although biological differences do exist, most of the Great Lakes species are morphologically very similar, inhabit nearly all parts of the lakes below the thermocline, and spawn at almost the same seasons. Laboratory experiments on Great Lakes *Coregonus* have demonstrated that some of the species are completely interfertile (Garside and Christie 1962; L. E. Cable unpublished data; T. N. Todd unpublished data) — a finding that agrees with similar work on European coregonines (Kajosaari 1957; Gasowska 1958; Svardson 1957, 1958, 1965). Our approach to species recognition is therefore pragmatic and basically phenetic; populations are considered valid species if they are phenotypically different from one another and

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such differences can be inferred to be genetically and not environmentally based. However, if research demonstrates that the morphological differences between two supposed species are primarily the result of environmental effects during development, the two kinds should be considered as one species.

Coregonus zenithicus is the most easily identified species of cisco in Lake Superior, having a longer snout, shorter fins, and fewer and shorter gillrakers than the other species. Also, the lower jaw is included within the upper jaw, and the premaxillaries are more nearly vertical than those of the other species. Two previously recognized species, *C. nigripinnis cyanopterus* and *C. reighardi dymondi*, have phenotypes which are almost identical to that of *C. zenithicus*. Morphological and biological differences are noticeable among several populations of *C. zenithicus*, and some populations appear to be more distinct from one another than they are from previously recognized species of ciscoes.

We suspected that *C. zenithicus*, *C. n. cyanopterus*, and *C. r. dymondi* were one species. The limited geographic distributions of *cyanopterus* and *dymondi* suggested that the slight morphological differences between them and *zenithicus* might be the result of environmental effects during development. Similar differences were previously observed by Koelz (1929) and Todd et al. (1981) artificially reared coregonines and by Hile (1937) in different year-classes of *C. artedii* in some small Wisconsin lakes. Our objectives in the present study were to analyze morphological variability in several geographically distinct samples of *C. zenithicus* (presumably representing local populations) and to compare these samples with those of *C. n. cyanopterus* and *C. r. dymondi.*

Materials and Methods

We examined 298 fish from the University of Michigan Museum of Zoology (UMMZ) and four fish from the U.S. National Museum (USNM). The nominal species, number of fish, collector, and deposition of the collections were as follows:

Coregonus nigripinnis cyanopterus — 26, L. Superior off Grand Marais, Mich., October 3, 1917, W. Koelz, UMMZ 52870; 1, L. Superior off Marquette, Mich., USNM 64672.

C. reighardi dymondi — 1, L. Superior 34 km W of Ontonagon, Mich., August 24, 1921, W. Koelz, UMMZ 53626; 7, L. Superior Thunder Bay, Ont., September 17, 1923, W. Koelz, UMMZ 54601; 18, L. Superior Thunder Bay, Ont., November 25, 1922, W. Koelz, UMMZ 59181, 59230, 59238, 59242, 59245, 59247, 59252, 59254, 59317, 59318, 59322; 1, L. Superior off Rossport, Ont., March 10, 1922, W. Koelz, UMMZ 54581; 5, L. Superior off Moffat Strait, Ont., September 25, 1923, UMMZ 54612–54615, 54621; 4, L. Superior off Salter Is., Ont., October 29, 1923, W. Koelz, UMMZ 54616-54619; 3, L. Superior Black Bay, Ont., July 20, 1922, W. Koelz, UMMZ 57377, 57397, 57399; 1, L. Superior Armour Harbor, Ont., August 5, 1922, W. Koelz, UMMZ 57793; 2, L. Superior off Grand Marais, Minn., September 14, 1921, W. Koelz, UMMZ 53798, 53761; 2, L. Superior between Cat and S. Twin Is., Wisc., July 11, 1922, W. Koelz, UMMZ 58180, 58183; 5, L. Superior off Ontonagon, Mich., August 24–25, 1921, W. Koelz, UMMZ 53603, 53606, 53609, 53614, 53755; 24, L. Nipigon off Macdiarmid, Ont., July 26, 1922, W. Koelz, UMMZ 57250, 57259, 57261, 57262, 57265, 57267, 57269-57273, 57285, 57286, 57288, 57290, 57298, 57301, 57302, 57304, 57306, 57309, 57312, 57321; 1, L. Nipigon off Macdiarmid, Ont., July 26, 1922, W. Koelz, USNM 88353.

C. reighardi reighardi — 3, L. Michigan off Washington Is., Wisc., August 18, 1920, W. Koelz, UMMZ 5440; 4, L. Michigan off Michigan City, Ind., September 3, 1920, W. Koelz, UMMZ 54464; 5, L. Michigan off Charlevoix, Mich., August 21, 1923, W. Koelz, UMMZ 62542, 62564, 62583; 1, Lake Michigan off Michigan City, Ind., April 1, 1921, W. Koelz, USNM 87351.

C. zenithicus — 26, L. Superior off Marquette, Mich., August 8, 1921, W. Koelz, UMMZ 53375, 53382, 53393, 53396, 53403, 53408, 53409, 53412, 53414, 53422, 53428, 53432–53434, 53436, 53438, 53447, 53449, 53473, 53474, 53477, 53486, 53494, 53496, 53498; 23, L. Superior Alona Bay, Ont., June 22, 1922, W. Koelz, UMMZ 57057-57060, 57062, 57063, 57065, 57069, 57071, 57076, 57087, 57091, 57097, 57105, 57129, 57137; 2, L. Superior Agawa Bay, Ont., June 19, 1922, W. Koelz, UMMZ 57054, 57056; 1, L. Superior Port Coldwell, Ont., October 23, 1923, W. Koelz, UMMZ 59835; 11, L. Superior off Rocky Is., Wisc., July 15, 1922, W. Koelz, UMMZ 58335, 58337, 58340, 58341, 58351, 58359, 58361, 58386, 58425, 58437, 58442; 7, L. Superior off S. Twin Is., Wisc., July 14, 1922, W. Koelz, UMMZ 57185-57190, 57192; 5, L. Superior off S. Twin Is., Wisc., July 15, 1922, W. Koelz, UMMZ 58246, 58248, 58267, 58298, 58309; 26, L. Superior Thunder Bay, Ont., September 15, 1923, W. Koelz, UMMZ 57848; 19, L. Nipigon off Macdiarmid, Ont., July 25, 1922, W. Koelz, UMMZ 57256-57258, 57263, 57264, 57266, 57274, 57287, 57296, 57305, 57308, 57320, 57322, 57329, 57327, 57329, 57337, 57343, 57340; 24, L. Superior off Copper Harbor, Mich., May 16, 1974, S. Kauppi, UMMZ 205323; 12, L. Superior W. of Portage Channel on Keweenaw Peninsula, Mich., May 14, 1974, J. Wiita, UMMZ 205324; 2, L. Superior Keweenaw Bay, Mich., May 15, 1974, P. Jarvi, UMMZ 205325; 3, L. Superior off Copper Harbor, Mich., May 15, 1974, W. Jamsen, UMMZ 205326; 3, L. Superior Keweenaw Bay, Mich., December 17, 1974, P. Jarvi, UMMZ 205327; 4, L. Superior W. of Keweenaw Portage Channel, Mich., December 19, 1974, J. Wiita, UMMZ 205328; 7, L. Superior off Marquette, Mich., December 18, 1974, F. Thill, UMMZ 205329; 6, L. Superior off Stockton Is., Wisc., May 24, 1974, USFWS, UMMZ 205330; 2, L. Superior off Presque Isle Pt., Wisc., November 28, 1973, USFWS, UMMZ 205331; October 2, 1974, USFWS, UMMZ 205332; 1, Lake Superior off Isle Royal, Mich., September 1908, USNM 62517.

The 29 morphological and meristic characters which follow were obtained for each fish: standard length, gillraker number, lateral line scales, head length, occiput length, dorsal base, anal base, dorsal–adipose distance, adipose–caudal distance, body depth, body width, snout–dorsal dis-

TABLE 1. Comparison of some morphometric characters of *C. nigripinnis* and *C. zenithicus*.[a]

	C. n. nigripinnis (Lakes Michigan and Huron)		*C. n. cyanopterus* (Lake Superior)		*C. zenithicus* (Lake Superior)		*C. reighardi dymondi* (Lake Superior)	
Character	$\bar{x}$	95% C.I.	$\bar{x}$	95% C.I.	$\bar{x}$	95% C.I.	$\bar{x}$	95% C.I.
Gillraker number	47.1	1.9	40.4	0.7	40.2	0.9	36.8	0.9
Standard length/head length	4.1	0.3	4.1	0.1	4.0	0.1	3.9	0.1
Head length/snout length	3.7	0.3	3.7	0.2	3.5	0.2	3.8	0.1
Head length/eye diameter	4.1	0.1	4.4	0.1	4.4	0.1	4.0	0.1
Head length/gillraker length	5.2	0.9	5.5	1.4	6.0	1.9	5.7	0.2

[a]Data taken from Koelz (1929).

tance, snout–anal distance, eye diameter, maxillary length, snout length, mandible length, adipose height, gillraker length, pectoral–ventral distance, anal–ventral distance, dorsal height, anal height, pectoral length, ventral length, dorsal rays, anal rays, pectoral rays, and ventral rays. Gillraker length was taken from the median gillraker and measured using an ocular micrometer in a dissecting microscope and other measurements were made using vernier calipers. The characters chosen represent morphometric features commonly used to identify coregonines. We followed the methods of Koelz (1929) in making the individual counts and measurements. Ages were determined from scales of 26 *C. nigripinnis cyanopterus* collected off Grand Marais and 26 *C. zenithicus* collected off Marquette (both are Michigan ports).

Morphological and meristic data were analyzed by principal-component analysis and distance coefficients. Following Sneath and Sokal (1973) and Blackith and Reyment (1971), we used the principal components to produce graphical projections of the specimens along axes that summarized the correlated information among all of the characters. Previous work has shown that samples of fishes representing distinct, closely related species will usually cluster without overlap on principal-component projections if an adequate number of characters are employed (Smith 1973; Todd et al. 1981).

The distance coefficient used in this study, the mean character difference (M.C.D.), is often called the "city-block" metric (Sneath and Sokal 1973). It is calculated by the following equation:

$$\text{M.C.D.} = 1/n \sum_{i-1}^{n} | X_{ij} - X_{ik} |$$

where n is the number of taxonomic characters, j and k represent different individuals, and i represents the characters.

Lengths of the fish differed substantially in the groups of fish we chose to compare. We eliminated (or at least minimized) the confusing effect of length differences in the calculation of the distance coefficients by using character values adjusted for allometric differences by the following formulas (Thorpe 1975):

$$\hat{\hat{Y}}_i = 10^{\hat{Y}_i}$$

$$\hat{Y}_i = \log_{10} Y_i - b(\log_{10} X_i - \log_{10} \bar{\bar{X}}),$$

where b is the regression coefficient of $\log_{10} Y$ against $\log_{10} X$ (calculated separately for each group we analyzed); $\hat{\hat{Y}}_i$ is the adjusted character value for the ith specimen; $\hat{Y}_i$ is the logarithm of the adjusted character value of the ith specimen; Y_i is the unadjusted character value of the ith specimen; and X_i is the standard length of the ith specimen; $\bar{\bar{X}}$ is the grand mean of standard length for all specimens in the analysis.

The adjusted character values for each of 28 variables (standard length was not used in the data set of adjusted values) were then standardized for the calculation of the distance coefficients by the formula:

$$Z = (\hat{\hat{Y}}_i - \bar{\bar{\hat{\hat{Y}}}})/s$$

where Z is the standardized value of the variable; $\hat{\hat{Y}}_i$ is the adjusted character value for the ith specimen; $\bar{\hat{\hat{Y}}}$ is the mean adjusted character value; and s is the standard deviation of the character. Standardizing the data removed the effect of magnitude from the calculations, so that characters with very large values were not disproportionately represented in the calculation of mean character difference.

Similarity of Populations

Koelz (1929) recognized *Leucichthys nigripinnis cyanopterus* as a subspecies endemic to Lake Superior. Jordan and Evermann (1911) previously considered this fish to be a distinct species, *Leucichthys cyanopterus*. Subsequently, *Leucichthys* has been included within *Coregonus* (Norden 1961). Koelz reported it to have fewer gillrakers, a longer head and snout, a smaller eye, a more elongated body than *C. n. nigripinnis*, which was found only in Lakes Michigan and Huron, and a lower jaw that was usually shorter than or equal to the upper jaw. Also, the pigmentation was different from that of *C. n. nigripinnis*, "being not very different from that recorded for *zenithicus* of Superior" (Koelz 1929). In contrast, *C. n. nigripinnis* of Lakes Michigan and Huron was a large, heavy-bodied, and darkly pigmented fish differing from *C. n. cyanopterus* and *C. zenithicus* in gillraker number, eye diameter, and pigmentation (Table 1). *Coregonus n. cyanopterus* appears to be distinct from *C. n. nigripinnis* but not so from *C. zenithicus*.

Coregonus reighardi dymondi of Lakes Nipigon and Superior was separated from *C. r. reighardi* of Lakes Michigan and Ontario by its proportionally longer head, snout, maxilla, and paired fins, and smaller eye and deeper body, along with less pigment (especially

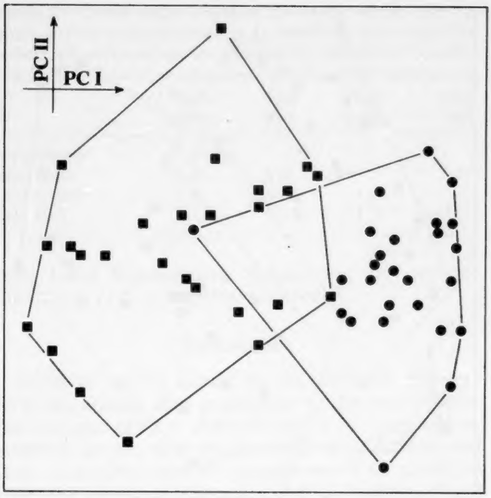

FIG. 1. Ordination of principal components I and II. *Coregonus zenithicus* (■) and *C. nigripinnis cyanopterus* (●).

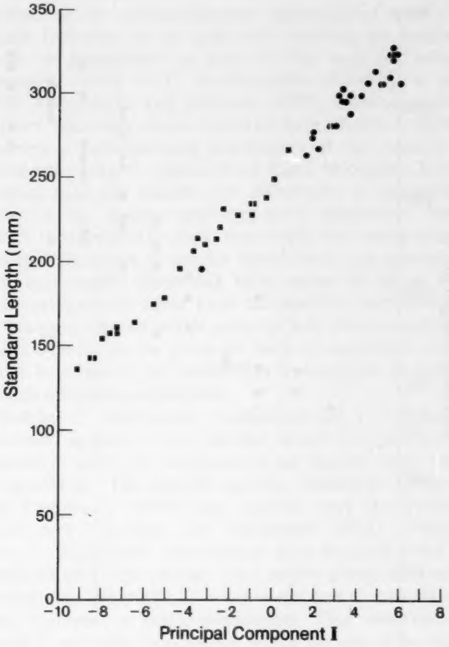

FIG. 2. Principal component I vs. standard length for *C. nigripinnis cyanopterus* (●) and *C. zenithicus* (■).

on the tips of the snout and lower jaw) (Koelz 1929). Also, *C. r. dymondi* spawned in late fall whereas *C. r. reighardi* spawned in spring.

While *C. r. dymondi* was distinct from *C. r. reighardi* it was less so from *C. zenithicus*, being distinguished by such features as a shorter snout, fewer gillrakers, and a larger eye (Koelz 1929). Gillraker number had a mean difference of 3.4 gillrakers between Lake Superior *C. r. dymondi* and *C. zenithicus* (Table 1) which was comparable to that observed between laboratory-reared coregonines and their wild-caught parents (Todd et al. 1981). Likewise, snout length and eye diameter have been shown to have a significant environmental component in their development (Todd et al. 1981).

Principal-component analysis of *C. n. cyanopterus* and *C. zenthicus* from eastern Lake Superior showed no differences — except horizontally along principal component I, which merely reflected differences in size (Fig. 1 and 2). Moreover, the size difference between these two forms was found to be due to age (Fig. 3). The specimens of *C. n. cyanopterus* were older than the specimens of *C. zenithicus*, and of the size expected for old *C. zenithicus*. Little doubt remains that *C. n. cyanopterus* and *C. zenithicus* were separated on the basis of allometric differences in size-related characters and that in reality they were collected from populations of the same species.

Principal-component analysis of data for *C. r. dymondi* and *C. zenithicus* from Thunder Bay resulted in clusters with some overlap (Fig. 4). The amount of overlap and the parallel nature of the clusters resemble patterns found between wild parents and their laboratory-reared progeny in a previous study (Todd et al. 1981). This similarity suggested that the species were not distinct and that the morphological differences between them were probably attributable to environmental differences during development.

Geographic Variation

We analyzed six Lake Superior populations by comparing distance coefficients between and within populations, including four populations of *Coregonus zenithicus* and one each of *C. nigripinnis cyanopterus* and *C. reighardi dymondi* (Fig. 5). Using Student's t-test, within-group distances were significantly lower ($P < 0.001$) than between-group distances, indicating some geographic localization and differentiation of populations.

The low within-group mean distances of Thunder Bay *C. r. dymondi* and *C. zenithicus* suggest that these two species are in reality a single population. Such low values can result from an artificial division of a single population into two morphs, since the variability within each morph is decreased by such a division. The Thunder Bay populations are significantly less variable than any of the others, and thus conform to expecta-

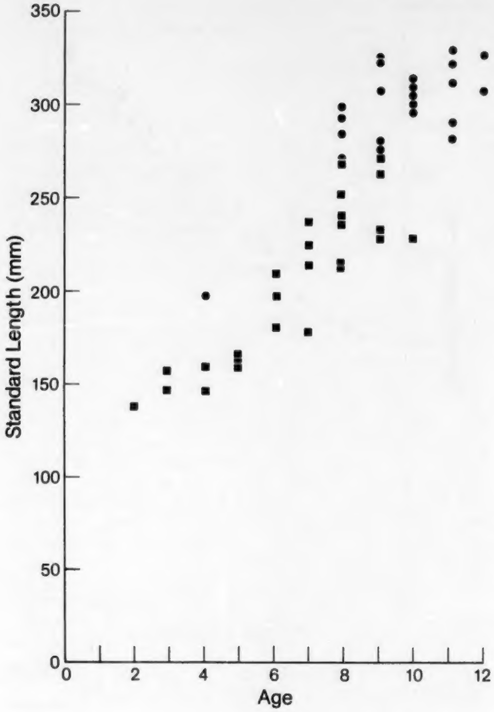

FIG. 3. Age vs. standard length. *Coregonus zenithicus* (■) and *C. nigripinnis cyanopterus* (●).

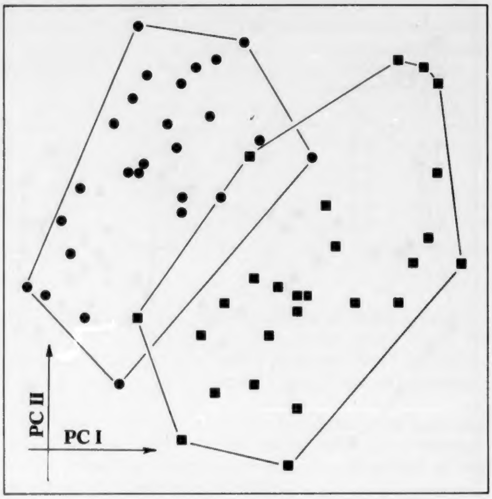

FIG. 4. Ordination of principal components I and II. *Coregonus zenithicus* (■) and *C. reighardi dymondi* (●) from Thunder Bay, Ont.

tion for a population divided by an error in sampling.

We compared distance coefficients from samples of spring and fall spawning *C. zenithicus* from eastern Lake Superior (Keweenaw Peninsula area to Marquette) and western Lake Superior (Apostle Islands) (Table 2). Distance values for all within- and between-group comparisons were surprisingly similar. This similarity could have been caused by heterogeneous samples, because the eastern fish were taken from more than one locality. Also, small sample sizes may have obscured geographic variation. The magnitude of the observed values is the same as that observed for geographically distant populations of *C. zenithicus* (Fig. 5), and suggests that the time of spawning is no more important than geographic isolation in the differentiation of populations.

Examination of the relationships of *C. r. dymondi* and *C. zenithicus* from Lake Superior with *C. r. dymondi* and *C. zenithicus* from Lake Nipigon (the type locality for *C. r. dymondi*) and with *C. r. reighardi* from Lake Michigan (the type locality for *C. r. reighardi*), using distance coefficients demonstrate geographic localization as well as two levels of differentiation (Table 3). The distance coefficients for *C. r. dymondi* and *C. zenithicus* from Lakes Superior and Nipigon are all very similar (0.95–1.1) and significantly lower than those for comparisons with *C. r. reighardi* from Lake Michigan. This evidence suggests that *C. zenithicus* and *C. r. dymondi* are conspecific. The greater distance values associated with *C. r. reighardi* reveal that *C. r. reighardi* is at least more distinct than any of the populations of *C. zenithicus* or *C. r. dymondi*

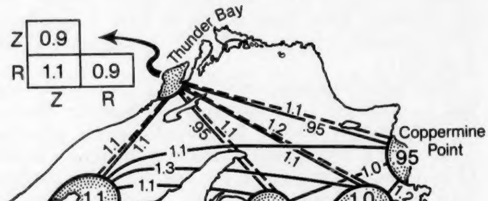

FIG. 5. Geographical representation of taxonomic distances (grand mean of character differences) within and among several populations in Lake Superior. Solid lines indicate distances among populations of *C. zenithicus* (and *C. nigripinnis cyanopterus*, a single population from Grand Marais, Michigan). Dashed or broken lines indicate distances between the Thunder Bay *C. reighardi dymondi* and the other populations. Abbreviations: R = *reighardi* and Z = *zenithicus*. The small distance matrix at upper left contains the coefficients for two Thunder Bay samples.

TABLE 2. Grand mean character differences within and between spawning populations of *C. zenithicus* from Lake Superior. All unlike values are significantly different ($P < 0.05$).

	West Spring	West Fall	East Spring	East Fall
West Spring	1.0			
West Fall	1.0	1.0		
East Spring	1.0	1.06	1.0	
East Fall	1.1	1.1	1.1	1.1

from Lakes Superior and Nipigon and may indicate the validity of *C. r. reighardi* as a species.

Systematics

Different species should be more distinct (distant) from one another than populations of the same species. Our samples of *C. r. dymondi* and *C. n. cyanopterus*, however, are no more distinct from *C. zenithicus* and from each other than are populations of *C. zenithicus* from one another — suggesting that *C. r. dymondi* and *C. n. cyanopterus* are not distinct species.

Populations of *C. zenithicus* can be characterized by biological as well as by morphological differences, since at least two populations differ in spawning time. The best-known populations spawn in November–December, but numerous observations of fish spawning in May–June have been made during the last 25 yr. The spring spawners seem to be most abundant near the Keweenaw Peninsula but have been collected from the Apostle Islands, Wisconsin, as well as off Grand Marais, Michigan. The abundance of spawning *C. zenithicus* in the spring suggest that these fish represent a distinct population(s) and not just random out-of-season spawners as Koelz (1929) concluded from the few ripe fish he collected in the spring.

The reproductive isolation inherent in nonoverlapping spawning times argues for recognition of the two groups at the species level. This view is extreme, however, because spawning time may be as variable as morphological characters. In *C. albula*, a European species, different populations spawn at different times of the year (Svardson 1949, 1957, 1970; Airaksinen 1967; Lind and Turunen 1968). Svardson (1979) described a new species, *Coregonus trybomi*, primarily because of its nonoverlapping reproduction with *C. albula*. However, in the case of *C. trybomi*, the species could be polyphletic as may be the case for some sympatric forms of *C. clupeaformis* (Lindsey et al. 1970; Kirkpatrick and Selander 1979). Similar to the disjunct spawning times reported here, Smith (1964) reported a fall-spawning population of the normally spring-spawning *C. reighardi* of Lake Michigan. Considering that the reasons for differences in spawning time are not known and that such differences may occur independently and repeatedly in coregonines makes recognition of species based solely on spawning time inadvisable. Spawning time seems to be in the same category as other local adaptations documented for coregonines and in this group of fish, at least, species status should not be given to each recognizable sympatric population, any more than it should be assigned to each allopatric population.

Neither *C. nigripinnis cyanopterus* nor *C. reighardi dymondi* appear to be distinct from *C. zenithicus*. Specimens of *C. n. cyanopterus* are merely large, old *C. zenithicus*. The specific epithet, *zenithicus* (Jordan and Evermann 1909), has priority over the epithet *cyanopterus* (Jordan and Evermann 1911). Therefore, *C. nigripinnis cyanopterus* may be considered a synonym of *C. zenithicus*. Low within-group distances suggest that sympatric *C. r. dymondi* and *C. zenithicus* may represent a single population. This observation coupled with distance values which do not differ significantly from those for populations of *C. zenithicus* make recognition of *C. r. dymondi* inadvisable. The specific epithet *zenithicus* (Jordan and Evermann 1909) has priority over either the specific epithet *reighardi* (Koelz 1924), or the subspecific epithet *dymondi* (Koelz 1929). Therefore, *C. r. dymondi* can be considered a synonym of *C. zenithicus*.

Management Implications

Although, at best, the species of *Coregonus* seem to rank as no more than semispecies (Svardson 1979), populations of morphologically, ecologically, and genetically similar forms may be reasonably grouped together and recognized as species. Usually little information other than morphology is available, but this may be sufficient for management purposes.

TABLE 3. Grand mean character differences within and between populations. All unlike values are significantly different ($P < 0.005$).

	C. r. reighardi (L. Michigan)	*C. zenithicus* (L. Superior)	*C. r. dymondi* (L. Superior)	*C. zenithicus* (L. Nipigon)	*C. r. dymondi* (L. Nipigon)
C. r. reighardi (L. Michigan)	0.9				
C. zenithicus (L. Superior)	1.4	0.9			
C. r. dymondi (L. Superior)	1.3	1.0	0.9		
C. zenithicus (L. Nipigon)	1.6	1.0	1.1	0.9	
C. r. dymondi (L. Nipigon)	1.7	1.1	1.1	0.96	0.8

The existence of morphologically distinct stocks within the species *C. zenithicus* is demonstrated by the results of this study. The size of coregonine stocks and the amount of genetic isolation among them are currently poorly known. Recent studies of *C. clupeaformis*, however, reveal that some local populations have distinct centers of abundance and yet have large overlapping distributions which may approach 160 km (Imhof 1977; Leary 1979). On the other hand, Smith and Van Oosten (1940) noted that tagged coregonines traveled no farther than 80 km from the point of tagging. Bays seem to be particularly effective in isolating populations, often harboring apparently distinctive stocks (Imhof 1977; Roelofs 1958). Low within-group distance coefficients of populations from bays, e.g. at Coppermine Point (Ontario), suggest the distinctiveness of these stocks. The populations of *C. zenithicus* previously known as *C. reighardi dymondi* occur almost entirely in the northern bays of Lake Superior.

Ciscoes in the Great Lakes should be managed as local stocks or populations, and not as widespread populations. Failure to do so results in serious depletion. For example, in the 1920s the lake herring, *Coregonus artedii*, was commercially exterminated in Lake Erie. Unaware of the local nature of coregonine populations, commercial fishermen converged upon an unusually concentrated aggregation of lake herring and so effectively harvested them that the fishery collapsed and has never recovered (Van Oosten 1930). Historically, fishermen fished a given area heavily and then moved on to new fishing grounds when the catches declined. Koelz (1929) and Van Oosten (1929) pointed out the damaging effect of such stock-ignorant practices following the move of Lake Erie fishermen to the other Great Lakes following the collapse of the Lake Erie fishery for lake herring. Similar tactics led to the virtual collapse of the Lake Huron chub fishery in the 1960s (Smith 1970; Eshenroder, R. 1974. A review of the chub fishery in Michigan's waters of Lake Huron in the years 1957 to 1968 and observations on the current status of stocks. Minutes of Lake Huron Committee, Great Lakes Fishery Commission. Appendix II b:27-37.).

Until more is known about the distribution of coregonine populations, management efforts might best concentrate on specific localities. These localities might well be delineated by utilizing both depth and fishing districts.

Acknowledgments

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Isolation and Identification of an Atypical *Aeromonas salmonicida* Strain Causing Epizootic Losses Among Atlantic Salmon (*Salmo salar*) Reared in a Nova Scotian Hatchery

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PATERSON, W. D., D. DOUEY, AND D. DESAUTELS. 1980. Isolation and identification of an atypical *Aeromonas salmonicida* strain causing epizootic losses among Atlantic salmon (*Salmo salar*) reared in a Nova Scotian hatchery. Can. J. Fish. Aquat. Sci. 37: 2236–2241.

The bacterium causing 50% cumulative mortality among postyearling parr (pyp) Atlantic salmon (*Salmo salar*) reared at a Nova Scotian hatchery was identified to be an atypical, achromogenic *Aeromonas salmonicida* strain. This organism, although differing in several biochemical reactions from typical *A. salmonicida*, was sensitive to *A. salmonicida* bacteriophages. Antigenically, the Kejimkujik *A. salmonicida* was indistinguishable from typical *A. salmonicida* strains when the serological relatedness was examined using cross-adsorbed rabbit antisera. Analysis of DNA from the atypical *A. salmonicida* yielded a % GC value of 57.85, a value within the range expected for *A. salmonicida*.

Key words: atypical, *Aeromonas salmonicida*, Atlantic salmon

PATERSON, W. D., D. DOUEY, AND D. DESAUTELS. 1980. Isolation and identification of an atypical *Aeromonas salmonicida* strain causing epizootic losses among Atlantic salmon (*Salmo salar*) reared in a Nova Scotian hatchery. Can. J. Fish. Aquat. Sci. 37: 2236–2241.

La bactérie responsable d'une mortalité cumulative de 50% chez les tacons de plus d'un an (pyp, « postyearling parr ») de saumon atlantique (*Salmo salar*) élevés dans un établissement de pisciculture de la Nouvelle-Écosse a été identifiée comme lignée atypique achromogène d'*Aeromonas salmonicida*. Bien que différant de *A. salmonicida* typique par plusieurs réactions biochimiques, cet organisme est sensible aux bactériophages de *A. salmonicida*. Sous le rapport des antigènes, *A. salmonicida* de Kejimkujik peut se différencier des lignées typiques de *A. salmonicida*, quand les relations sérologiques ont été examinées à l'aide d'antisérums de lapin contre-adsorbées. L'analyse de l'ADN chez *A. salmonicida* atypique donne une valeur GC, en pourcentage, de 57,85, ce qui est dans la gamme anticipée de *A. salmonicida*.

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IN the past, fish hatcheries of Canada's Atlantic region have not been plagued by furunculosis disease (McCraw 1952; Herman 1968) and the severe losses it causes. Recently, however, this disease has occurred in two Maritime locations. During the fall of 1975 and 1976, low water levels and high temperatures contributed to form the proper predisposing factors leading to furunculosis infections and heavy mortality in returning adult Atlantic salmon (*Salmo salar*) on the Restigouche River, New Brunswick (Weber and Zwicker 1979). Restigouche River outbreaks were caused by a typical pigment-producing strain of *Aeromonas salmonicida*.

In 1974, abnormally high mortalities occurred in underyearling parr (uyp) and postyearling parr (pyp) Atlantic salmon reared at the Federal Kejimkujik Fish Culture Station, Kejimkujik National Park, Nova Scotia. This report documents this epizootic, the clinical signs encountered and the characteristics of the atypical organism responsible for the outbreak.

Materials and Methods

Atlantic salmon uyp and pyp were examined for external disease signs. Samples aseptically removed from external body lesions or kidney were cultured at 22°C on trypticase soy agar (TSA) enriched with 5% sheep blood. These isolations yielded pure cultures of similar bacteria designated Kejimkujik SK_1, Kejimkujik JuvA, Kejimkujik 1A, and Kejimkujik SL_1, which were further characterized for more complete identification. Reference strains used in the identification were *Aeromonas salmonicida* ATCC 14174, *A. hydrophila* ATCC 14715 and *Haemophilus piscium* ATCC 15711.

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Logarithmic phase cells were harvested from Brain Heart Infusion agar (BHIA) (DIFCO Laboratories Detroit, MI) slants and washed once in 0.85% saline prior to use as inocula for biochemical characterization tests. The procedures followed are outlined in the Manual of Clinical Microbiology (Blair et al. 1970). Phase contrast microscopy observation of moist mount preparations was used to determine motility. Electron microscopy of phosphotungstic acid-stained preparations was utilized to examine the bacteria for presence of flagella.

The effect of pH and salt concentration on bacterial growth was determined using BHIA plates incubated at 22 and 28°C. Sensitivity of the bacterial isolates to discs containing various antibacterial agents was determined on BHIA plates incubated at 22°C. The double agar layer procedure (Adams 1959) was used to observe the relative sensitivity of the isolates to three *A. salmonicida* bacteriophages designated 37, 40 RR2·8t and 59.1 (Paterson et al. 1969).

To compare the serological relatedness of the Kejimkujik strain to *A. salmonicida*, antisera against Kejimkujik 1A, *A. salmonicida* ATCC 14174, *A. hydrophila* ATCC 14715, and *Haemophilus piscium* ATCC 15711 were produced in rabbits in response to an intravenous-intraperitoneal injection schedule of formalin-killed bacterial suspensions. The antigenic relationship of the Kejimkujik strain to other selected bacteria was determined by microtiter agglutination titrations of cross adsorbed rabbit antisera with various *Aeromonas* antigens. Serum adsorption and microtiter agglutination procedures were performed as described by Paterson et al. (1980).

The base composition of deoxyribonucleic acid (DNA) isolated from the Kejimkujik 1A isolate according to procedure of Marmur (1961), was estimated from its buoyant density in cesium chloride (Schildkraut et al. 1962). The buoyant density determination was carried out in a Beckman Model E centrifuge using *Micrococcus luteus* DNA as a reference.

Results

HISTORICAL

The federal fish culture station located within Kejimkujik National Park in southern Nova Scotia receives its surface water supply from Grafton Lake. The culture practice within this station focused on raising Atlantic salmon from eggs to smolts. These anadromous fish are then released for their sea phase of life.

At this station, water temperature maxima often ranged between 20 and 25°C during the growing season from June to September. Hatchery records indicate that abnormally high mortalities occurred during June of 1970 in specific ponds of pyp Atlantic salmon. A preliminary investigation of this problem tentatively identified the cause as *Haemophilus piscium* (R. Hyatt personal communication), the causative agent of ulcer disease. Similar infections had also been reported at other federal hatcheries during 1970. The cumulative mortality of pyp was not excessive during this period (Fig. 1) but many animals in specific ponds demonstrated black discoloration and suffered mortality. In the fall of 1973, some Atlantic salmon exhibited surface ulcers or lesions (R. Eisner personal communication) but no further diagnostic work was initiated at that time to identify the cause of the problem.

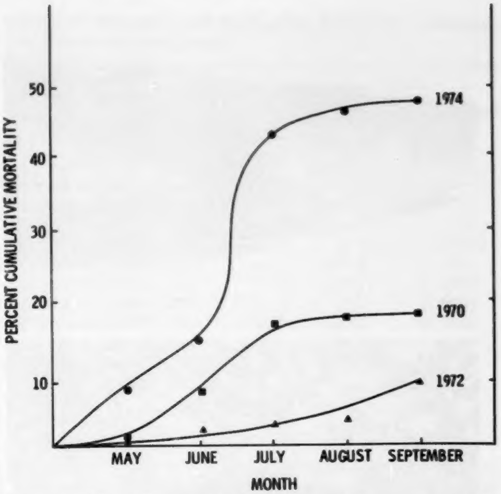


FIG. 1. Cumulative mortality of postyearling parr Atlantic salmon at Kejimkujik Fish Culture Station 1970–74.

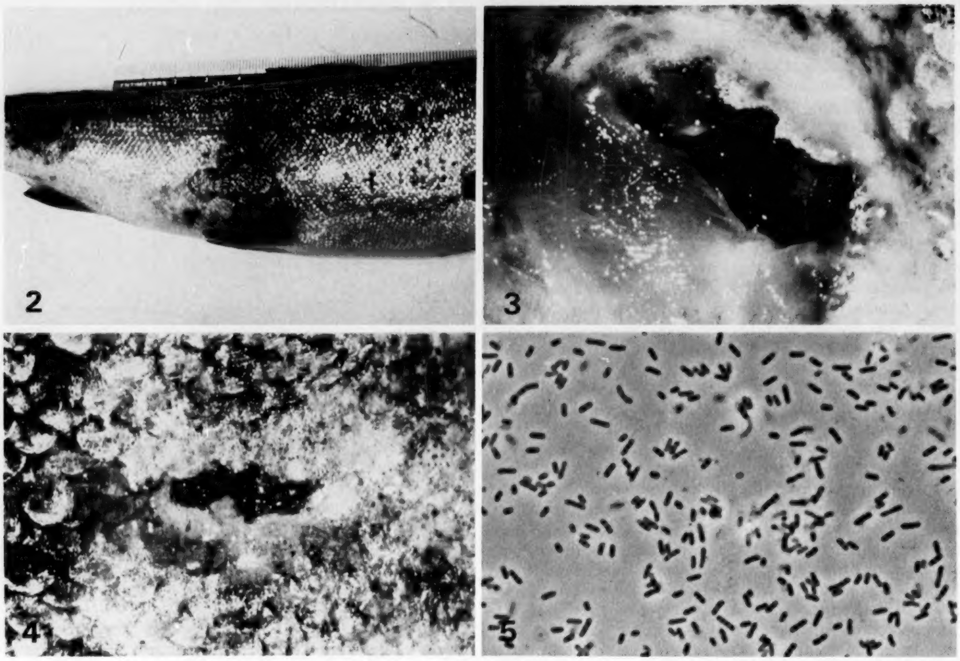
In 1974, excessive mortalities were first observed in May among pyp Atlantic salmon and as the summer progressed, an epizootic of unknown cause killed nearly half of these valuable animals (Fig. 1). In addition to the presence of badly eroded dorsal fins, many of the animals exhibited external body lesions or ulcers (Fig. 2, 3, 4). The external sores ranged in appearance from a small superficial wound with little necrosis to deep jagged lesions surrounded by necrotic muscle.

BACTERIAL ISOLATION

Pure cultures of a slow growing, nonmotile, Gram negative rod-shaped isolate were obtained from lesions and kidneys of uyp and pyp Atlantic salmon cultured on TSA + 5% sheep blood (Table 1). Culture of these organs on unenriched TSA was unsucccessful. No isolations were made from kidneys of salmonid and nonsalmonid fish sampled from either Grafton Lake (the hatchery water source) or from Mill Brook (the stream receiving the hatchery effluent).

ISOLATE CHARACTERIZATION AND IDENTIFICATION

The bacterial cultures isolated from the Kejimkujik fish were similar in appearance and physiology. Optimum growth occurred at 28°C with no growth at 37°C. With repeated transfer, adequate growth of this fastidious isolate was obtained on BHI media without sheep blood enrichment. Morphologically, 48-h cells of this isolate from BHI broth were round-ended, aflagellate, non motile, Gram negative rods. Phase con-



FIGURES 2–5

FIG. 2. Atlantic salmon post yearling parr with body lesion caused by *Aeromonas salmonicida* (Kejimkujik isolate); FIG. 3. Deep necrotic lesion ×10; FIG. 4. Shallow abrasion-like sore ×10; FIG. 5. *Aeromonas salmonicida* Kejimkujik cells isolated from kidney and lesions of infected fish. Note polar bodies present in many cells. (Phase contrast microscopy of a broth culture moist mount ×1500.)

trast microscopy of moist mount preparations made from 24 h broth cultures demonstrated the presence of terminal polar bodies in many of the cells (Fig. 5). The Kejimkujik isolates produced indole, produced acid from sucrose, did not reduce nitrates to nitrites and did not produce a water soluble brown pigment (Table 2). A typical *A. salmonicida strain* (ATCC 14174) produced opposite results in all of these particular tests. The fastidious nature of the Kejimkujik organism did not allow evaluation of amino acid requirements.

The Kejimkujik isolates SK_1, JuvA, 1A, and SL_1 were all sensitive to the *A. salmonicida* bacteriophages 37, 44 RR2·8t and 59.1 (Paterson et al. 1969) (Table 3). The relative efficiency of plating (EOP) for these cultures was lower than values obtained for the reference strain *A. salmonicida* ATCC 14174. We attribute these lower EOP values to lighter lawns resulting from slower growth but further investigations are required in this area. Rapid growth of these Kejimkujik strains necessary for production of confluent bacterial lawns and bacteriophage sensitivity assay was achieved only by using inocula prepared by daily transfer in BHI broth.

The Kejimkujik isolate was serologically indistinguishable from *A. salmonicida* ATCC 14174 (Table 4). The autoagglutinating nature of the Kejimkujik isolates did not allow their use as an agglutinating antigen but they were used to produce specific rabbit antisera and

TABLE 1. Isolation of atypical *A. salmonicida* in Nova Scotia 1974.

		No. atypical *A. salmonicida* isolations from	
Source	Species	Kidney	Lesions
Hatchery	Atlantic salmon	7/18	6/18
Grafton Lake	Brook trout	0/1	no lesions
(Hatchery source)	Nonsalmonid	0/51	
Mill Brook	Atlantic salmon	0/7	
(Below hatchery)	Brook trout	0/5	no lesions
	nonsalmonid	0/1	

TABLE 2. Characteristics of the Kejimkujik isolate (an atypical *A. salmonicida*).

Cell appearance	Gram negative round-ended rod with polar bodies
Motility	—
Presence of flagella	—
Temperature range	slow at 10°C optimum 28°C no growth at 37°C
Growth on enriched agar	small 0.5 mm raised colonies in 4–7 d
Production of indole, catalase and cytochrome oxidase	+
Utilization of glucose	fermentative
Production of acid from glucose, maltose, galactose, trehalose, mannitol, and sucrose	+
Sensitive to erythromycin terramycin (slight) and chloromycetin (chloramphenicol)	+
Optimum pH	7–8
Sensitive to *Aeromonas salmonicida* bacteriophages 37, 40 RR_2·8t and 59.1	+
Pigment production	—
Nitrates reduced to nitrites	—
DNA base composition (% GC)	57.85

TABLE 3. Sensitivity of Kejimkujik isolates to *Aeromonas salmonicida* bacteriophages.

	Relative[a] EOP[b] with *Aeromonas salmonicida* phages		
Culture	Phage 37	Phage 40 RR_2·8t	Phage 59.1
Aeromonas salmonicida ATCC 14174	100	100	100
Kejimkujik isolate SK_1	2.5	0.77	0.00002
Kejimkujik isolate JuvA	41.3	11.9	0.023
Kejimkujik isolate 1A	1.8	25.7	0.0075
Kejimkujik isolate SL_1	9.2	1.2	0.0004
H. piscium ATCC 15711	16.1	96.8	0.0086

[a] *A. salmonicida* ATCC 14174 = Reference strain.
[b] EOP = Efficiency of plating.

to adsorb other antisera. The following treatments were unsuccessful in altering the autoagglutinating nature of this isolate: suspension in distilled water rather than saline, sonication, heating to 56°C and growth in presence of Tween 80.

Cesium chloride equilibrium centrifugation of DNA isolated from the Kejimkujik isolate revealed a buoyant density of 1.7167 and a % GC of 57.85 (Table 2).

Discussion

Although this Kejimkujik isolate utilized sucrose,

TABLE 4. Serological relatedness of the Kejimkujik isolate to *Aeromonas salmonicida* ATCC 14174, *Aeromonas hydrophila* ATCC 14715 and *Haemophilus piscium* ATCC 15711.

		Titer with various antigens	
Antiserum	Adsorbing antigens	*A. salmonicida* ATCC 14174	*A. hydrophila* ATCC 14715
Aeromonas salmonicida ATCC 14174	None	10 240	160
	A. salmonicida ATCC 14174	—[a]	40
	Kejimkujik isolate JuvA	—	40
	A. hydrophila ATCC 14715	2 240	—
Kejimkujik isolate 1A	None	15 760	80
	A. salmonicida ATCC 14174	—	—
	Kejimkujik isolate JuvA	—	—
	A. hydrophila ATCC 14715	5 120	—
Aeromonas hydrophila ATCC 14715	None	—	5120
	A. salmonicida ATCC 14174	—	1280
	Kejimkujik isolate JuvA	—	5120
	A. hydrophila ATCC 14715	—	80
Haemophilis piscium ATCC 15711	None	20 480	80
	A. salmonicida ATCC 14174	—	—
	Kejimkujik isolate JuvA	—	—
	A. hydrophila ATCC 14715	1 920	—

[a] Titer of <20 or 20 denoted by —.

produced indole, did not liquify gelatin or reduce nitrate or produce water soluble brown pigment, physiological features quite uncharacteristic of typical *A. salmonicida* strains, data presented herein suggest that this isolate is an atypical *A. salmonicida*. As with typical strains of *A. salmonicida* it was sensitive to *A. salmonicida* bacteriophages, was serologically indistinguishable from *A. salmonicida* ATCC 14174 and contained DNA with a G + C ratio similar to *A. salmonicida* (McCarthy 1978).

The number of reports regarding infections caused by atypical *A. salmonicida* is growing and there are indications that problems caused by these strains may differ from those caused by typical strains in terms of host range, geographic distribution and clinical signs produced (Ajmal and Hobbs 1967; Bootsma et al. 1977; Evelyn 1971; Hastein 1976; Hastein et al. 1978; Kimura 1969; Ljungberg and Johansson 1977; McCarthy 1975; Ojala 1966; and Shotts et al. 1980).

Hemophililus piscium, the causative agent of ulcer disease, has recently been identified as an atypical *A. salmonicida* (Paterson et al. 1980 and Tables 3 and 4).

Considering the clinical signs caused by infections of atypical strains, as in carp (Bootsma et al. 1977), goldfish (Shotts et al. 1980), or Atlantic salmon as reported here, it would seem worthwhile to designate the form of furunculosis found with a more descriptive name, such as ulcerative furunculosis.

The presence of atypical furunculosis in the province of Nova Scotia alters our previous conceptions of the distribution of this pathogen. Although we cannot make absolute inferences about the presence of furunculosis caused by an atypical *A. salmonicida* here in the past without diagnostic confirmation, there is hatchery evidence suggesting that abnormal losses occuring at this station may have been caused by this pathogen.

The present diagnostic procedures should be improved by using enriched media to facilitate the initial isolation of fastidious atypical *A. salmonicida* isolates such as the one described here. The difficulty in primary isolation of this organism and other similar pathogens (Bootsma 1977) using accepted diagnostic procedures (Gillespie et al. 1974) suggests that fish disease infections of this type could have gone undetected in the past. If this is so, the actual prevalence of furunculosis (caused by typical and atypical *A. salmonicida* strains) may be much larger than the recorded one.

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Seston Ecology of the Surface Waters of Hudson Bay

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ANDERSON, J. T., AND J. C. ROFF. 1980. Seston ecology of the surface waters of Hudson Bay. Can. J. Fish. Aquat. Sci. 37: 2242–2253.

The planktonic biomass variables, chlorophyll *a*, ATP, particulate organic carbon, and nitrogen have been measured in surface waters throughout Hudson Bay for the first time. On the basis of these variables Hudson Bay can be regarded as oligotrophic during the summer months. Clear inshore–offshore gradients of biomass were evident showing significant correlations in transects to salinity, temperature, depth, and distance from shore. Chlorophyll *a* values were always low, averaging 0.09 mg m^{-3} offshore and 0.28 mg m^{-3} inshore. ATP averaged 0.072 mg m^{-3} offshore and twice as high inshore. Biomass ratios also demonstrated clear inshore–offshore gradients; carbon:nitrogen ratios ranged from 4.9:1 inshore to 12.5:1 offshore indicating nitrogen limitation of offshore waters. Chlorophyll *a*: phaeopigment ratios decreased and biocarbon:chlorophyll *a* ratios increased offshore indicating an increased proportion of heterotrophs and possibly higher relative grazing pressure offshore. For the inshore areas, biomass and probably productivity were highest and significantly correlated to runoff with the exception of the Southampton–Coats–Mansel islands area, which is influenced by waters from Foxe Channel and Hudson Strait. While Hudson Bay meets most of the criteria for arctic classification, its character is sufficiently different to warrant special status.

Key words: Hudson Bay, seston ecology, chlorophyll *a*, biomass ratios, phaeopigments, plankton

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Les variables de biomasse planctonique, chlorophylle *a*, ATP, carbone organique particulaire et azote, ont été mesurées pour la première fois dans les eaux de surface de toute la baie d'Hudson. D'après ces variables, on peut considérer la baie d'Hudson oligotrophe pendant les mois d'été. Des gradients de biomasse, de la côte vers le large, sont bien en évidence, avec corrélations significatives en coupe avec la salinité, la température, la profondeur et la distance du rivage. Les valeurs de chlorophylle *a* sont toujours faibles, 0,09 mg m^{-3} au large et 0,28 mg m^{-3} près de la côte en moyenne. L'ATP est en moyenne de 0,072 mg m^{-3} au large et deux fois plus élevée près du rivage. Les rapports de biomasse démontrent également la présence de gradients bien définis, de la côte vers le large; les rapports carbone:azote s'étalent de 4,9:1 à la côte à 12,5:1 au large, signe d'une limitation d'azote des eaux du large. Les rapports chlorophylle *a* phaeopigment diminuent et les rapports biocarbone:chlorophylle *a* augmentent vers le large, indiquant une production accrue d'hétérotrophes et possiblement un broutage relativement plus intense au large. Dans les régions côtières, la biomasse et probablement la productivité sont maximales et montrent une corrélation significative avec le ruissellement, sauf dans la région des îles Southampton, Coates, et Mansel, influencée par les eaux du chenal Foxe et du détroit d'Hudson. Bien que la baie d'Hudson satisfasse à tous les critères d'une classification arctique, son caractère diffère suffisamment pour justifier un statut spécial.

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HUDSON Bay is one of the last major oceanic areas to be studied. Previous biological investigations have been sporadic, geographically restricted, and mostly confined to species descriptions (see Beals and Shenstone 1968). Until the recent studies by Anderson et al. (1980) and Gerrath et al. (1980), only two reports on phytoplankton in the bay existed: a small survey of net plankton by Davidson (1931) and a more comprehensive study by Bursa (1961). Bursa's study however was mostly limited to the very northern part of Hudson Bay (Grainger and Dunbar 1956).

Invertebrates have received more attention (Grainger 1968), but emphasis has been on inshore benthic forms, with benthos representing 210 of 260 species identified. Similarly, the study of fisheries has been limited mostly to coastal areas, especially around the major rivers (Vladykov 1933; Hunter 1968). Early studies of the bay (Hachey 1931; Huntsman 1931) led to various

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interpretations of the oceanographic data. At one point, opinions on commercial fisheries ranged from, "... there are plenty of commercial fish ..." to "... Hudson Bay is a desert sea ..." (Bajkov 1975).

Activities presently underway, including oil exploration and large-scale hydroelectric developments, will continue to affect Canada's northern waters. Background studies on biological oceanography now exist for some northern areas, including the Beaufort Sea, Davis Strait, and waters around Baffin island, but Hudson Bay remains largely unknown. Primary production and biomass of plankton, and seston composition have never been measured in Hudson Bay with the recent localized exceptions of Legendre and Simard (1979) and Roff et al. (1980), and the trophic status of the bay is not adequately defined.

The purpose of the present study was to rectify some of these oceanographic deficiencies by investigating inter alia the composition and distribution of planktonic biomass in surface waters of Hudson Bay, and to establish its trophic status. The work was undertaken during 1975 when the Canadian Hydrographic Service initiated a multidisciplinary study of Hudson Bay. This presented a unique opportunity to sample the entire area of the bay on a spatial and temporal frequency never before possible. This paper therefore describes the sestonic environment of Hudson Bay for the first time. Cruise details and original data are available from Anderson (1979).

Description of the Study Area

Hudson Bay is the largest inland sea in the world, being approximately 8.14×10^5 km^2 (Prinsenberg 1977b); it is characterized as a gently sloping basin surrounded by a low shoreline. In spite of its considerable area Hudson Bay is relatively shallow, averaging about 120 m in depth and not exceeding 300 m. The bay is connected with the deeper waters of Hudson Strait by deep channels passing on either side of Coats and Mansel islands.

The drainage area of Hudson Bay is immense, draining approximately 31% of Canada's land mass. It covers a total area of 3.1×10^6 km^2 (Prinsenberg 1977b), reaching as far west as the Rocky Mountains and, to the south, as far as the Mississippi drainage basin. James Bay and its entire watershed empty into Hudson Bay in the southeast. The drainage basin extends through nearly 13 degrees of latitude, draining many types of topography ranging from arctic tundra to northern boreal forest. From this drainage basin, together with net precipitation, comes an estimated annual freshwater influx of 8.4×10^{11} m^3 of water, approximately 0.86% of the total volume of Hudson Bay (Prinsenberg 1977b). The hydrologic system of Hudson Bay therefore gives it the character of an enormous estuarine basin (Collin 1966).

The general surface circulation of Hudson Bay has been inferred from the early drift bottle studies of Hachey (1931, 1935). This is characteristically a cyclonic circulation with waters entering Hudson Bay between Southampton and Coats islands, circling the bay and exiting on either side of Mansel Island. Tidal influences enter Hudson Bay in the vicinity of Coats and Mansel islands, progressing in a westerly direction. At this point tides average 3.1 m above chart datum (Dohler 1968). The tidal effect is amplified on the west coast with vertical displacement being as great as 4 m in Churchill Harbour, while on the east coast tidal flux is much reduced, being as small as 0.5 m.

Onlv during the mid-1940s (Hare and Montgomery 1949), was it learned that Hudson Bay completely freezes over each winter. Previously it was assumed the bay remained ice-free except for the large area of shorefast ice, up to 113 km wide (U.S. Hydrographic Office 1946). Hudson Bay then, "..... is the largest body of water in the world that virtually freezes over each winter and becomes ice-free during the summer" (Prinsenberg 1977b). This ice cover is typified by stable shorefast ice and shifting ice sheets offshore, shore leads developing and disappearing with the prevailing winds. Ice thickness averages 1.5 m (Danielson 1971) with rafted ice rising from 1.8 to 6.1 m above the ice surface (Lardner 1968).

Ice break-up occurs first in southern James Bay beginning sometime in May. By late June, James Bay is virtually ice-free. Ice begins to break-up and clear from Hudson Bay towards the end of June to early July, with lowest ice concentrations being reported first north and east of the Ottawa–Belcher islands chain (Danielson 1971). Extensive areas of ice cover, mostly due to wind drift, usually persist along the southwest coast well into August. Presently it is known that Hudson Bay is subject to intense vertical stratification during the summer (Prinsenberg 1977a); it is believed that only partial mixing occurs in the fall (Collin 1966), with the bay becoming vertically homogeneous possibly to a depth of 60 m (J. Helbig, S. Prinsenberg, personal communication).

Materials and Methods

Between August 7 and September 23, 1975, 158 samples for total seston, salinity and temperature were collected from the surface waters of Hudson Bay. Sampling was carried out on a 24-h basis using a pumped plankton sampler model EG-169 (Heidt 1975, unpublished data) designed and constructed at the Canada Centre for Inland Waters, Burlington, Ontario. Incoming water was diverted to a sampling reservoir before passing through the pump, thereby reducing damage to organisms. The pump was run for 5 min (approximately 2× reservoir replacement time) before taking samples, to avoid between-sample contamination. The water intake was located near the bow, approximately 3 m below the water line.

Water samples were drawn from the reservoir and partitioned for phytoplankton, ash-free dry weight, particulate organic carbon–organic nitrogen, chlorophyll *a*, ATP, and salinity. Reeve Angel 984H glass fibre filter papers were used for all filtrations.

Conductivity was measured with an Autosal salinometer (Guildline Model 8400) calibrated with standard Copenhagen seawater. Salinity values were calculated from the conductivity ratio by Bennett's equation as reported by Perkin and Walker (1971). Measurements of temperature and salinity were made simultaneously with a T–S profiler as reported by Prinsenberg (1977a); temperature was also measured in the pumped sampler tank with a mercury thermometer.

ATP extraction was based on methods outlined by Holm-Hansen and Booth (1966). Three 100-mL samples were filtered in succession and extracted for 5 min in 5.0 mL of boiling TRIS buffer (0.02 mol/L; pH 7.75). Samples were analyzed with a Lab Line ATP photometer, Model No. 2000, using enzyme-substrate extract from Dupont's ATP reagent kit (Cat. no. 760145). For the bioluminescence reaction, 0.2 mL of sample was added to 0.1 mL of extract and following a 15-s delay, ATP was determined as the total emission through the succeeding 60-s period. The procedure was standardized using Grade I (Sigma) disodium crystalline adenosine 5′-triphosphate.

Chlorophyll *a* samples were filtered in duplicate and extracted in 90% acetone, and pigment concentrations were calculated from SCOR/UNESCO equations following procedures of Strickland and Parson (1972). In most cases 4 L of seawater were filtered. Samples were either analyzed spectrophotometrically aboard ship or were stored frozen at −20°C. Determination of possible loss of chlorophyll *a* from frozen samples was made and the subsequent corrections were applied to all chlorophyll *a* values (Anderson 1979).

Particulate organic carbon (POC) and particulate organic nitrogen (PON) were analyzed using a Hewlett Packard CHN Analyzer, Model 185, following the procedure of the Water Quality Section, C.C.I.W., Burlington, Ontario (O. El Kei personal communication). Up to 4 L of water was filtered as necessary; samples were stored until analysis at −20°C. Duplicate and blank determinations were carried out on approximately every tenth sample. Tests were standardized using cyclohexane −2:4 dinitrophenylhydrazine.

Measurements for dry weight (DW) and ash-free dry weight (AFDW) were made following the procedure of Strickland and Parsons (1972). After filtration of up to 4 L of water, filters were oven dried for 30 min at 75°C and stored in a desiccator. After weighing, samples were ashed at 550°C for 4 h and then reweighed, ash-free dry weight being calculated as loss-on-ignition. All samples were weighed on a Cahn electrobalance, Model G-2.

For all particulate measurements, the coefficients of variation (CV) for replicate samples ranged from 12.7% (PON) to 20.8% (chlorophyll *a*).

Results

Clear inshore–offshore gradients in physico-chemical and biological variables existed in Hudson Bay; in general biomass decreased and ecological maturity increased offshore. Within the inshore region, six areas were subjectively demarcated based on biomass values, biomass ratios, salinity–temperature distributions, phytoplankton data (Anderson et al. 1980; Gerrath et al. 1980), corresponding watershed areas and known duration of winter ice cover. The six areas recognized (Fig. 1) were:

1) the Chesterfield Inlet area
2) the west coast area, north of the Churchill River
3) the southwest coast, from the Churchill River to James Bay
4) the Belcher Islands area, north of the James Bay–Hudson Bay boundary and west of the Belcher and Sleeper islands
5) the Southampton–Coats–Mansel islands area, around these islands and contiguous with Hudson Strait
6) the northeast coast area, between Mansel Island and the Ottawa Islands.

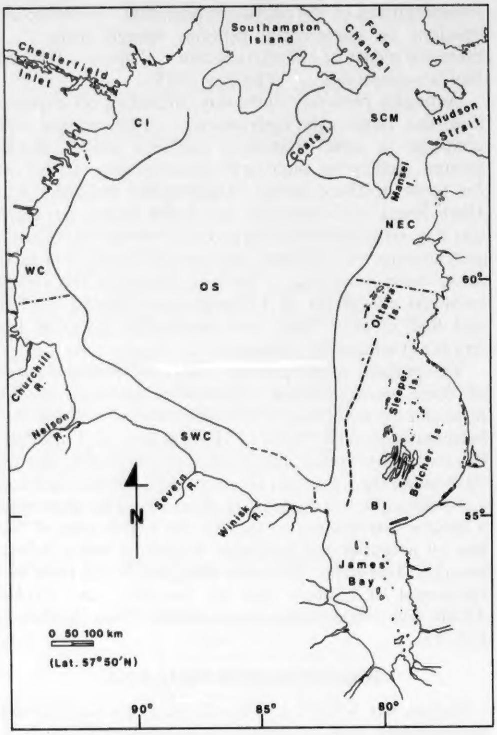


FIG. 1. Study area showing division of Hudson Bay into offshore (OS) and inshore regions, and the six areas of the inshore region: CI = Chesterfield Inlet, WC = west coast, SWC = southwest coast, BI= Belcher Islands, NEC = northeast coast, SCM = Southampton–Coats–Mansel islands. Dashed line north of Winisk river indicates a mixed area of uncertain affinity. Dashed line through BI area separates a section of high biomass west of the Belcher islands.

The inshore areas of Hudson Bay subject to higher freshwater runoff (taken from Prinsenberg 1977b) had significantly lower salinities and temperatures and significantly higher chlorophyll *a* ($P < 0.05$).

PHYSICAL VARIABLES

Salinities at 3 m depth in Hudson Bay ranged from 22.0 to 31.8‰. Highest salinities were found inshore around Coats and Southampton islands, and offshore near the middle of the bay (Fig. 2). Lower salinities were found in all inshore areas except the west coast area; here salinities of 29‰ were similar to those in the adjacent offshore region. The lowest salinities (<23‰) were found very close to shore, adjacent to the Nelson River. South of the Belcher Islands was a relatively large body of water of 25‰ salinity.

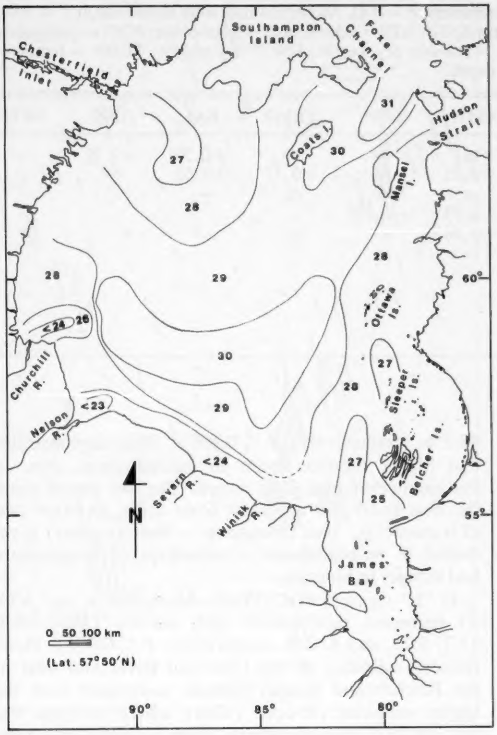

Southampton Island
Foxe Channel
Chesterfield Inlet
Hudson Strait
Coats I.
Mansel I.
Ottawa Is.
Sleeper Is.
Belcher Is.
James Bay
Churchill R.
Nelson R.
Severn R.
Winisk R.
N
0 50 100 km
(Lat. 57°50'N)
90°
85°
80°
60°
55°
31
30
27
28
29
30
29
28
<24
26
<23
<24
27
28
27
25

FIG. 2. Surface salinity distribution in Hudson Bay, August–September 1975. Figures are mean values, thus 29 = 28.5–29.5‰.

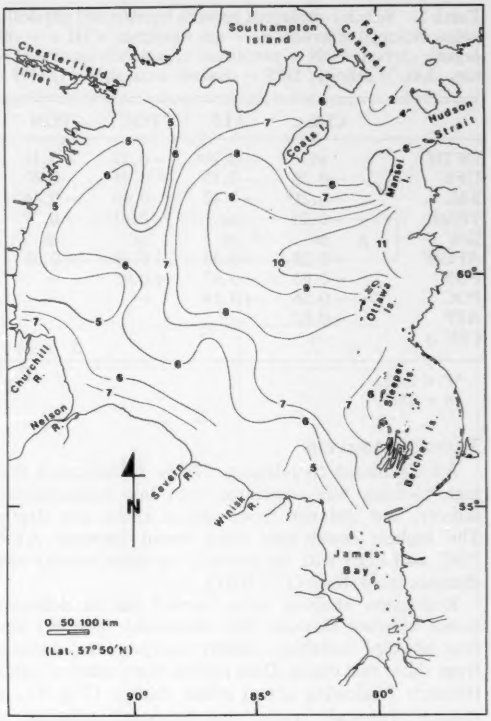

Southampton Island
Foxe Channel
Chesterfield Inlet
Hudson Strait
Coats I.
Mansel I.
Ottawa Is.
Sleeper Is.
Belcher Is.
James Bay
Churchill R.
Nelson R.
Severn R.
Winisk R.
N
0 50 100 km
(Lat. 57°50'N)
90°
85°
80°
60°
55°
2
4
5
6
7
8
9
10
11

FIG. 3. Surface temperature (°C) distribution in Hudson Bay, August–September 1975.

Temperatures at 3 m ranged mostly from 4.0 to 11.9°C, with two observations of 1.5°C east of Southampton Island during late September (Fig. 3). Low temperatures were also observed in the Chesterfield Inlet plume, along the west and southwest coast areas, and in the waters east of the Belcher Islands. A large area of higher temperatures, generally 8°C and above, was observed south of Coats and Mansel islands extending from the east coast far out into the Bay. Close to shore salinity and temperature were lower, and generally increased with distance from shore (Table 1).

TOTAL SESTON

Seston levels in Hudson Bay were higher closer to shore. Figure 1 is a composite diagram showing a line dividing inshore and offshore regions based on values of ATP, chlorophyll *a*, POC, and PON. The demarcation between inshore and offshore regions was most distinct for chlorophyll *a* and ATP (Table 2); of the two variables, chlorophyll *a* was the best discriminant (Fig. 4). Offshore values of chlorophyll *a* were always low, averaging 0.09 mg m^{-3}, while inshore values averaged 0.28 mg m^{-3}. ATP was more variable between the two regions (Table 2), averaging 0.072 mg m^{-3} offshore and 0.145 m^{-3} inshore.

Distributions of POC and PON at 3 m depth were similar to those of chlorophyll *a* and ATP; differences between inshore and offshore regions were smaller but nevertheless quite distinct (Table 2). Offshore POC averaged 0.053 g m^{-3} and PON averaged 0.006 g m^{-3}; inshore POC averaged 0.074 g m^{-3} and PON averaged 0.010 g m^{-3}. Ash-free-dry weight and dry weight both reflected the trend of higher values inshore, however, this was less distinct due to some mixing of high and low values in both inshore and offshore regions.

The highest correlations between biomass variables were found for ATP–PON, chlorophyll *a*–PON, and ATP–chlorophyll *a* (Table 1). As expected, lower coefficients were found for these variables with POC and AFDW, both of which include a detrital fraction. The high correlations of PON–POC and AFDW–DW are mostly a function of reduced variability due to simultaneous sampling.

TABLE 1. Simple correlations between biomass and physical parameters, $n = 130$. All correlations were significant at $P < 0.01$, unless indicated otherwise. ns = not significant; CHL *a* = chlorophyll *a*; ATP = adenosine 5′-triphosphate; POC = particulate organic carbon; PON = particulate organic nitrogen; AFDW = ash-free dry weight; DW = dry weight; TEMP = temperature; SAL = salinity; DFS = distance from shore; DPTH = depth.

	CHL *a*	ATP	POC	PON	AFDW	DW[b]	TEMP	SAL	DFS	DPTH
DPTH	ns	−0.20[a]	−0.33	−0.31	ns	ns	ns	+0.59	+0.71	—
DFS	−0.26	−0.33	−0.45	−0.49	−0.25	ns	+0.37	+0.50	—	
SAL	−0.21[a]	−0.47	−0.40	−0.44	ns	ns	ns	—		
TEMP	−0.26	ns	−0.23	−0.27	−0.33	−0.25	—			
DW	ns	ns	ns	ns	+0.76	—				
AFDW	+0.28	+0.24	+0.38	+0.38	—					
PON	+0.65	+0.67	+0.95	—						
POC	+0.56	+0.54	—							
ATP	+0.62	—								
CHL *a*	—									

[a] $P < 0.05$.
[b] $n = 79$.

TRANSECT ANALYSIS

All significant correlations (Table 1) indicated that high biomass was associated with low temperatures, salinity, and distance from nearest shore and depth. The highest coefficients were found between ATP, POC, and PON with the physical variables salinity and distance from shore ($P < 0.01$).

Regression analyses were carried out to delineate trends between biomass (the dependent variable) and four physical variables, salinity, temperature, distance from shore and depth. Data subsets were selected along transects (following actual cruise tracks) (Fig. 5), to reduce large-scale spatial and temporal variation, as indicated by residuals of the entire data set.

In all transects biomass increased closer to shore and adjacent to areas of high freshwater runoff. In "A" transect (Fig. 5) where ATP and salinity did not vary significantly, distance from shore was the most significant independent variable explaining variation in chlorophyll *a*, POC and PON ($R^2 = 67.1$, 52.9, and 42.2%, respectively, $P < 0.005$). This demonstrates that higher biomass exists in coastal areas, even in the absence of high land runoff. The low runoff from the west coast and northeast coast areas, at either end of transect "A" (see Discussion — Inshore areas) is reflected in nonsignificant relationships of temperature and salinity to biomass.

In "B" transect POC, PON, chlorophyll *a*, and ATP all regressed significantly with salinity ($R^2 = 76.5$, 75.7, 51.1, and 47.2%, respectively, $P < 0.005$). Here, reduced salinities off the Churchill River and west of the Belcher and Sleeper islands, contrasted with the higher salinities offshore (30‰) where biomass was low. In "C" transect where lower salinities and temperatures were found inshore, temperature was the most important variable associated with higher biomass, although decreasing salinities and depths were also significant. Regressions of ATP, PON, and POC gave R^2 values of 85.7, 82.2, and 77.2%, respectively ($P < 0.005$).

TABLE 2. Summary of biomass data from inshore and offshore regions. CHL *a* = chlorophyll *a*; ATP = adenosine 5′-triphosphate; POC = particulate organic carbon; PON = particulate organic nitrogen; AFDW = ash-free dry weight; DW = dry weight. (C.I. = 95% confidence interval of the mean.)

	CHL *a* (mg/m³)	ATP (mg/m³)	POC (g/m³)	PON (g/m³)	AFDW (g/m³)	DW (g/m³)
Inshore						
Mean	0.28	0.145	0.074	0.010	0.306	0.709
SD	0.21	0.073	0.024	0.003	0.105	0.222
C.I. ($P < 0.05$)	±0.05	±0.017	±0.006	±0.001	±0.025	±0.068
Maximum	1.08	0.461	0.178	0.023	0.682	1.630
Minimum	0.08	0.010	0.043	0.005	0.083	0.388
Offshore						
Mean	0.09	0.072	0.053	0.006	0.254	0.721
SD	0.04	0.001	0.021	0.003	0.118	0.484
C.I. ($P < 0.05$)	±0.01	±0.008	±0.005	±0.001	±0.026	±0.140
Maximum	0.29	0.174	0.190	0.021	0.995	3.548
Minimum	0.04	0.009	0.033	0.003	0.018	0.423

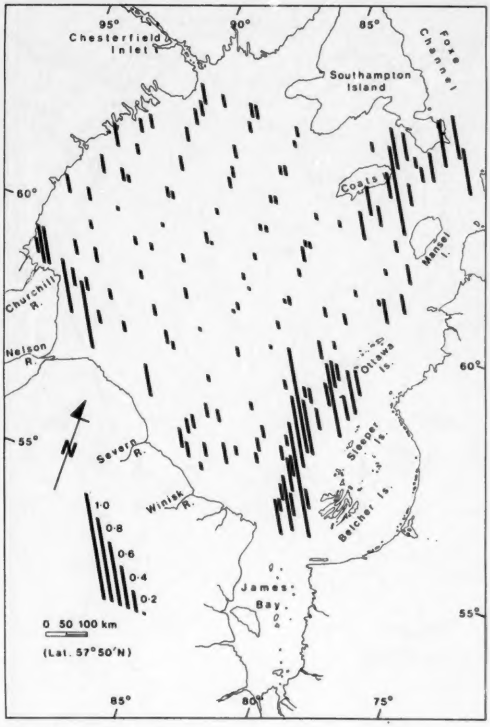

95°
Chesterfield Inlet
90°
85°
Foxe Channel
Southampton Island
Coats I.
60°
Mansel I.
Churchill R.
Nelson R.
Ottawa Is.
60°
55°
N
Severn R.
Sleeper Is.
Winisk R.
Belcher Is.
1.0
0.8
0.6
0.4
0.2
James Bay
55°
0 50 100 km
(Lat. 57°50'N)
85°
80°
75°

FIG. 4. Surface chlorophyll *a* (mg m^{-3}) distribution in Hudson Bay, August–September 1975. Station location is base of bar.

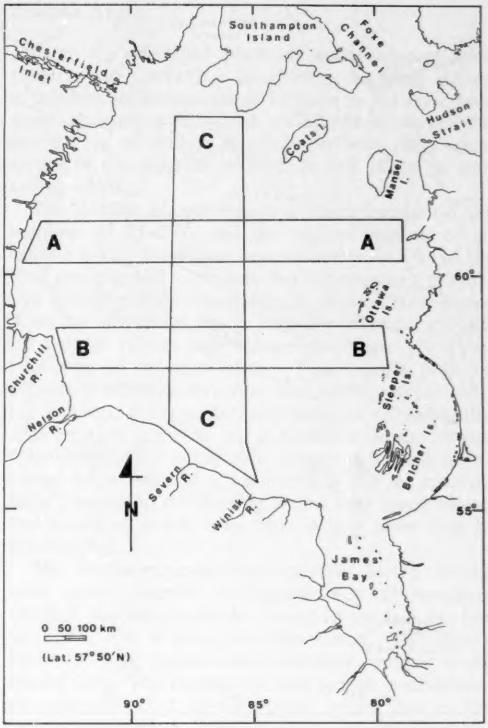

Southampton Island
Foxe Channel
Chesterfield Inlet
Hudson Strait
Coats I.
Mansel I.
C
A
A
60°
Ottawa Is.
B
B
Churchill R.
Sleeper Is.
Nelson R.
C
Belcher Is.
N
Severn R.
Winisk R.
55°
James Bay
0 50 100 km
(Lat. 57°50'N)
90°
85°
80°

FIG. 5. Transect locations in Hudson Bay.

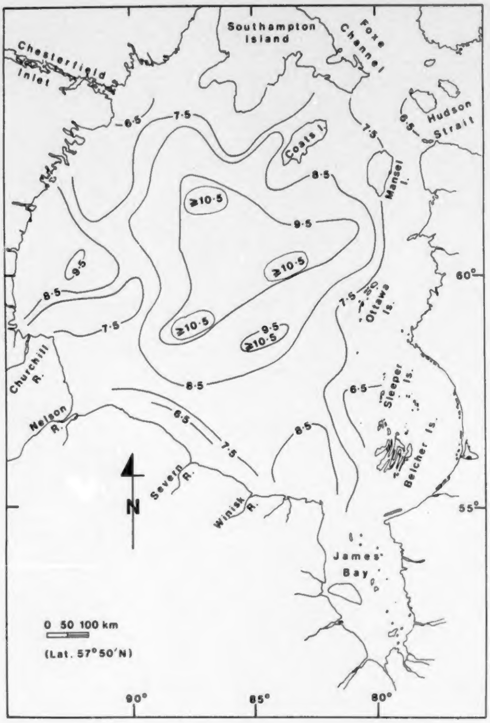
BIOMASS RATIOS

Biomass ratios in Hudson Bay showed inshore–offshore distributions similar to those of individual biomass variables. Carbon:nitrogen (C:N) ratios ranged from 4.9:1 inshore on the southwest coast, to values over 9.5:1 (maximum 12.5:1) found almost exclusively in the middle of the bay (Fig. 6). The overall average for the bay was 8.1:1. Most inshore areas had C:N ratios of 7.1:1 or less (Fig. 6); the exceptions were an inshore area near the Winisk River and the west coast area, which had values in the range of 8.1:1. Both these areas have higher salinities inshore.

Chlorophyll *a*:phaeopigment (CHL*a*:PHAEO) ratios in Hudson Bay averaged 7.2 overall and showed a very clear distribution pattern (Fig. 7). Higher values were found almost exclusively nearshore and low values offshore, with the exception of some very low values (down to 1.6) off the Churchill River, and regions of intermediate values in the northeast coast and west coast areas. Inshore values averaged 8.3, and reached a maximum of 30. Almost concentrically within this, a region with a mean ratio of 4.2 (range 2.2–10) was clearly defined. At the center of the bay was a large area showing a mean ratio of 1.5, with all ratios <2.5.

Biocarbon:chorophyll *a* (BIOC:CHL*a*) ratios (BIOC = ATP × 250, Holm-Hansen 1973b) averaged 233:1, and showed distinct areas of similar values (Fig. 8). Ratios for much of Hudson Bay ranged between 200:1–500:1, with stations at the center of the bay exceeding 500:1 (maximum 1014:1). The lowest ratios, ≤100:1 (minimum 60:1), were found in the Belcher Islands and Southampton–Coats–Mansel islands areas, and near the Churchill River. The remaining inshore areas were predominantly in the range of 200:1. The Hudson Strait area has been presented in Fig. 8 as having very low BIOC:CHL*a* ratios. More precisely, four stations here (August 18–19) gave values of 250–350:1, contrasting sharply with 10 later observations (September 19–22) all about 100:1. The difference was a result of increased chlorophyll *a* during September.

Values of BIOC:POC, expressed as a percentage, ranged from 10.5 to 156% with an average of 50.7%. High values (>50%) were found inshore along the southwest coast, with maximum values (>70%)


Southampton Island
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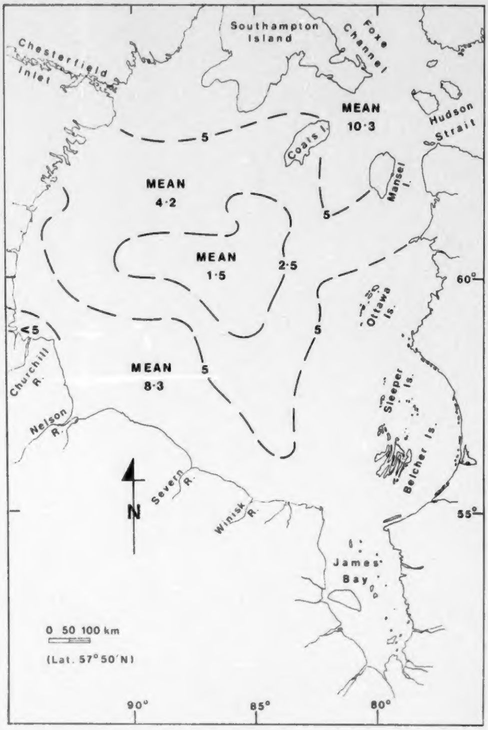
Ottawa Is.
Sleeper Is.
Belcher Is.
Churchill R.
Nelson R.
Severn R.
Winisk R.
James Bay
6·5
7·5
8·5
9·5
≥10·5
N
0 50 100 km
(Lat. 57°50′N)
60°
55°
90°
85°
80°

FIG. 6. Surface C:N (carbon:nitrogen) ratio distribution in Hudson Bay.


Southampton Island
Foxe Channel
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Hudson Strait
Coats I.
Mansel I.
Ottawa Is.
Sleeper Is.
Belcher Is.
Churchill R.
Nelson R.
Severn R.
Winisk R.
James Bay
MEAN 10·3
MEAN 4·2
MEAN 1·5
MEAN 8·3
5
2·5
<5
N
0 50 100 km
(Lat. 57°50′N)
60°
55°
90°
85°
80°

FIG. 7. Surface chlorophyll *a*: phaeopigment ratio distribution in Hudson Bay.

around the Belcher and Sleeper islands and in the Chesterfield Inlet plume. Much of the offshore region, and the Southampton–Coats–Mansel islands area, had values <50%.

Discussion

THE INSHORE–OFFSHORE GRADIENT

On the basis of differences in both biological and physico-chemical variables, Hudson Bay can be divided into inshore and offshore regions. The lower temperatures inshore are attributed to mixing processes which result in colder deep water being brought to the surface (S. Prinsenberg personal communication). Higher temperatures south of Mansel Island are attributed to more stable surface waters heated by solar radiation. Lower inshore salinities indicate the effects of freshwater runoff.

Inshore phytoplankton concentrations were higher in Hudson Bay (Anderson et al. 1980; Gerrath et al. 1980); a principal components and cluster analysis of the phytoplankton data (Rogers, Roff, and Anderson unpublished data) resolves a very similar division into inshore and offshore regions. Such a coastal gradient is in fact characteristic of most large bodies of water. The increase in nutrients, standing crop, and plankton production as the continental margins of oceans are approached is a well established phenomenon (Riley 1937; Riley and Chester 1971; Strickland 1965; Parsons et al. 1969; Ryther 1969; Sharp 1975; Yentsch 1975).

Several reasons for higher biomass and production in coastal waters have been advanced. Among these are: nutrient enrichment from freshwater runoff; nutrient entrainment from an incoming deep water layer and/or recirculation of nutrients within the inshore mixed layer; mixing from increased tidal and wind effects inshore; attenuation of coastal populations carried offshore; and, with respect to islands, the "island mass effect" of Doty and Oguri (1956).

Results of transect regression analysis indicated that in all cases biomass decreased away from shore. However, differences in the significance of the independent variables indicated varying relationships between

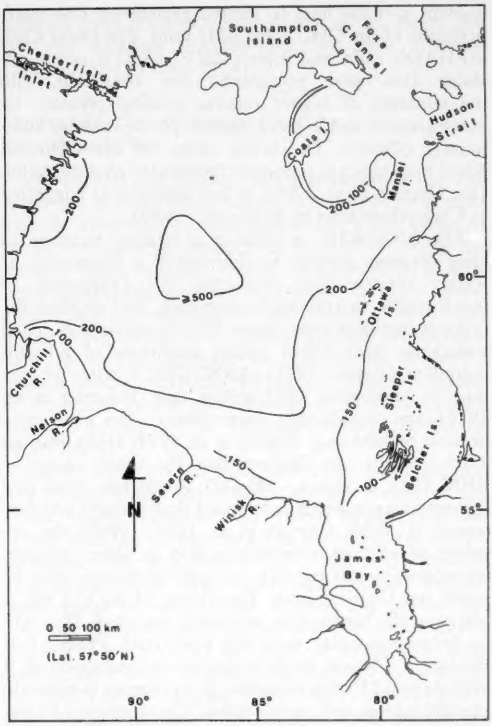

FIG. 8. Surface biocarbon:chlorophyll *a* ratio distribution in Hudson Bay.

physical variables and biomass in different areas of Hudson Bay. Overall the analysis indicated that biomass was a function of freshwater input (either due to direct nutrient additions, e.g. Sutcliffe [1972], or to deep water entrainment, e.g. Fournier et al. [1977]) whether described by salinity, temperature, distance from shore, or depth. This generalization did not extend to the Southampton–Coats–Mansel islands area where runoff was very low, and high salinities corresponded to high biomass (see next section). Thus it seems that land runoff and associated coastal circulation are the predominant factors influencing standing crop and probably productivity in the surface waters of Hudson Bay.

Since regression analysis indicated the decrease in biomass away from shore to be linear, it was not statistically possible to define a boundary between inshore and offshore regions, even though differences were significant. This boundary should therefore be considered simply as a practical demarcation distinguishing the highest biomass near the coast, where coastal influences predominate, from the lower biomass characteristic of the offshore region.

INSHORE AREAS

From the results of this study and Anderson et al. (1980), and Gerrath et al. (1980), we have elected to describe six inshore areas. Differences between these areas appeared to be related to land runoff, the circulation pattern of Hudson Bay, and probably the edaphic nature of the different watersheds and effects of prevailing winds.

The Belcher islands area was characterized by low salinities of 25–27‰ and the highest biomass of all inshore areas; it receives approximately 44.6% of the total yearly runoff to Hudson Bay (Prinsenberg 1977b). Due to the cyclonic circulation in Hudson Bay, waters from the southwest coast area are directed towards the Belcher Islands and "accumulate" here (N. Freeman personal communication). This, together with the effluent from James Bay, may lead to considerable mixing, resulting in higher biomass. Early in the spring this area receives relatively warm waters from an ice-free (Danielson 1971) James Bay, already at its peak spring runoff, while most of Hudson Bay is still ice covered. Thus production presumably begins here much sooner and continues much later than in any other area of Hudson Bay.

The southwest coast area receives 33.1% of the total annual runoff to Hudson Bay (Prinsenberg 1977b). Salinities were the lowest in the bay (as low as 22‰), but despite the huge runoff, low salinity water and high biomass were relatively confined to the coastal area. The reasons for this narrow confinement are speculative. It would appear to be due to the cyclonic circulation directing water eastward along the coast, and to a strong movement inshore of high salinity water at the surface. This is evident from the high salinity water (~30‰) adjacent to the southwest coast area, and the steep salinity gradient between inshore and offshore regions. The origin of this high salinity water mass is not known. Deep water moving south into the bay may be subject to upwelling in shallow waters at this point, or it may be due entirely to surface circulation characteristics.

The Chesterfield Inlet area extended as a distinct plume well out into Hudson Bay. This is no doubt attributable to the characteristics of surface water circulation, perhaps aided by predominantly offshore winds. Chesterfield Inlet accounts for 6.6% of the annual runoff into Hudson Bay (Prinsenberg 1977b). Biomass levels here were among the lowest of the inshore areas, probably attributable to the arctic tundra drained by its watershed. The plankton ecology of this area has recently been described by Roff et al. (1980); biomass values agree closely with those reported here.

The Southampton–Coats–Mansel islands area was unlike the other inshore areas in being subject to virtually no land runoff. This area is influenced by incoming high salinity waters from Hudson Strait and Foxe Channel. Waters in Hudson Strait are extremely well mixed (Dunbar 1958); Bursa (1961) reported a greater productivity in Hudson Strait as compared to northern Hudson Bay. It is likely that higher biomass values here are the result of transport into this area of both biomass and nutrients from Hudson Strait and Foxe Channel.

The west coast and northeast coast areas are both subject to low runoff, 3.9 and 3.1% of the total, respectively (Prinsenberg 1977b); consequently they had higher salinities, and lower biomass levels. The west coast area appears to be contiguous with offshore waters in its properties, and the northeast coast area is probably influenced from the south by Belcher Islands area waters.

BIOMASS RATIOS

C:N ratios in Hudson Bay approximated averages for Pacific Ocean surface waters of 8.7:1 (Sharp 1975, after Gordon 1971) and 8.5:1 (Holm-Hansen 1972), and compare to surface values in the North Atlantic (Menzel and Ryther 1964). The C:N average for Hudson Bay is lower than for surface waters of the Arctic Ocean sampled under the ice (Kinney et al. 1971; Holm-Hansen 1972), indicating more productive conditions in Hudson Bay, at least inshore.

Values of C:N ratios can reflect the proximate composition and nutrient status of seston. Low C:N ratios for phytoplankton have been reported from both cultures and natural populations to range from 3 to 7:1 by weight (Strickland 1960; Antia et al. 1963; Sutcliffe 1972; Banse 1974; Carpenter and Price 1977). Such values are typical for nonlimited growth phase populations. High C:N ratios can result from nitrogen limitation, influx of terrigenous material, or from increased detrital organic matter. Phytoplankton subjected to nitrogen limitation showed C:N ratios up to 15–25:1 (Eppley 1971; Banse 1974).

The low values inshore indicate less detrital material and, in relation to offshore regions, a greater proportion of viable cells (also indicated by lower BIOC:CHL *a* ratios). Such low ratios are probably attributable to higher nutrient availability inshore. The higher ratios of the west coast area and the coastal waters near the Winisk river probably indicate less productive areas of lower nutrient concentrations. The lower C:N ratios of the area north and east of Mansel island reflect the influence of more productive Hudson Strait and Foxe Channel waters. Higher C:N ratios in central Hudson Bay probably indicate nitrogen depletion. Phytoplankton biomass was low, as indicated by chlorophyll *a*, and the detrital fraction of the total seston increased (indicated by BIOC:POC ratios).

The CHL *a*:PHAEO ratio is known to increase with zooplankton grazing (Shuman and Lorenzen 1975), but significant correlations of zooplankton to this ratio may only occur in oligotrophic waters (Glooschenko et al. 1974). The ratio is also recognized as an index of algal cell senescence (Jensen and Sakshaug 1973). No attempt is made here to defend exclusively one interpretation of the CHL *a*:PHAEO ratio. The lower CHL *a*:PHAEO ratio and higher BIOC:CHL *a* ratios offshore (see next paragraph) are consistent with the concepts of higher relative grazing pressure by heterotrophs, and a more mature phytoplankton community offshore. The lower ratios off the Churchill River may indicate senescent freshwater phytoplankton (see Gerrath et al. 1980) at low salinities as suggested in Chesterfield Inlet by Roff et al. (1980).

The BIOC:CHL *a* ratio is a relative measure of "live" organic carbon, to chlorophyll *a*. Generally, as waters become less productive the proportion of heterotrophs to autotrophs increases, and so does the ratio. It increases from about 50:1 in nutrient enriched waters, to over 250:1 under conditions of nutrient limitation (Eppley 1971). BIOC:CHL *a* ratios of productive continental shelf waters (e.g. Fournier et al. 1977) are considerably lower than in less productive oceanic regions (e.g. Eppley et al. 1973; Holm-Hansen 1969, 1973b). In Hudson Bay the lower range of BIOC:CHL *a* values, 100–200:1 and less, indicated inshore areas in which autotrophs predominate (Anderson et al. 1980; Gerrath et al. 1980). While the absolute quantity of heterotrophs may be larger inshore, its proportion compared to the phytoplankton must be much less than offshore. The values of BIOC:CHL *a* are generally higher than previously reported. This may be because samples were not prefiltered. Prefiltration through a 150-μm mesh is commonly employed as a prelude to ATP determination, in an attempt to separate phytoplankton and zooplankton. The fraction of total heterotrophs removed by prefiltration is not known, but it may lower the ATP concentration by up to 2× (Pett and Roff unpublished data).

Ratios of BIOC:POC indicate the proportions of "live" and "dead" organic matter. In the euphotic zone of oceanic areas, values generally range from 20 to 90% (Holm-Hansen 1973a; Sutcliffe et al. 1970). In Hudson Bay, higher values were generally found inshore, especially in the Belcher Islands area and adjacent to the mouth of Chesterfield Inlet. Lower BIOC:POC values close to shore off the Churchill and Nelson rivers appear to be a function of higher detrital loads from these rivers, compared to Chesterfield Inlet. Low percentages of live seston were observed inshore in both the west coast area and in the region of the Winisk River. The BIOC:POC ratios indicate, as did C:N, BIOC:CHL *a* ratios and individual biomass variables, that both these inshore areas maintain a lower biomass possibly stemming from an intrusion of offshore water. The Southampton–Coats–Mansel islands area contrasted with other inshore areas. It appears to be relatively nutrient enriched, as indicated by C:N and BIOC:CHL *a* ratios, however, it is also subject to greater detrital loading, as evidenced by low BIOC:POC ratios. This detrital loading likely results from the more productive waters of Hudson Strait and Foxe Channel moving into Hudson Bay. Similar transport of detrital material from the productive waters of the North Sea into the adjacent Wadden Sea has been observed (Manuels and Postma 1974).

TROPHIC STATUS AND ARCTIC CLASSIFICATION OF HUDSON BAY

Chlorophyll *a* in Hudson Bay was generally low and below the average for subarctic and temperate oceans. Inshore, chlorophyll *a* approaches the upper range of values reported by Sutcliffe et al. (1970) from the western North Atlantic. Values of chlorophyll *a* measured around the Belcher Islands are in close agreement with those of Legendre and Simard (1979) from the same region. However, offshore values are substantially lower and resemble the low values of barren tropical seas, e.g. 0.04 to 0.07 mg m^{-3} in surface waters of the North Pacific gyre (Eppley et al. 1973), rather than the 0.5 mg m^{-3} of temperate oceans (Strickland 1960, 1965).

Similarly, values of POC and PON from Hudson Bay resemble the oligotrophic surface waters of the Pacific Ocean (Gordon 1971; Handa et al. 1972) and in the Atlantic, of the Sargasso Sea (Gordon 1970). In Hudson Bay the lower range of values is similar to most ocean areas, both neritic and oceanic, but the upper range of values from Hudson Bay seldom approaches the peaks reported for other ocean areas. For a specific comparison, the Gulf of Mexico, a large semienclosed body of water less than 200 m in depth, had POC values ranging from 0.022 to 1.911 g m^{-3} (Fredericks and Sackett 1970). The lower value is less than that observed in Hudson Bay, while the upper value is an order of magnitude greater. In contrast, POC and PON values from Hudson Bay are greater than those reported for both the oligotrophic waters of the South Atlantic (Hobson et al. 1973), and the Arctic Ocean (Kinney et al. 1971; Holm-Hansen 1972).

Several authors since Huntsman (1954) have considered Hudson Bay as a region of low productivity. The present biomass data, and the existence of a well developed subsurface chlorophyll maximum (Anderson and Roff unpublished data) throughout the offshore area of Hudson Bay, support this position.

Legendre and Simard (1979) suggested nitrogen limitation in Hudson Bay and demonstrated low nitrate levels (maximum 6.6 m g-at N-NO_3 m^{-3}) even in deep Hudson Bay waters. Nitrate levels in the Chesterfield Inlet area (Pett and Roff unpublished data) are very similar to those reported by Legendre and Simard (1979). Perhaps one of the most surprising features of Hudson Bay is that despite the enormous freshwater runoff (Prinsenbreg 1977b), the biomass supported is low. The low productivity of the bay may be due at least in part to its intense stratification, and the probability that the deepwater layer is only partially mixed with the surface layer each year. However, if this is the case then the low nitrogen levels in the subpycnocline layer are unexpected; further information on the deepwater mass of Hudson Bay is badly needed.

While Hudson Bay meets most of Dunbar's (1968) criteria for arctic classification, differences in latitude, ice break up times, light regime, hydrographic system, and biomass levels indicate that it should perhaps be placed in a unique category consistent with its estuarine basin character. In comparison to Grainger (1959) and Bursa (1961) who showed that in arctic waters peak production occurs in late July to August, peak production in Hudson Bay probably occurred earlier. Chlorophyll *a* levels in Hudson Bay never approached bloom conditions, and there was no evidence of seasonal changes in biomass from July to the end of September. Peak production in Hudson Bay probably occurs between May in the south and June in the north. A seasonal chlorophyll *a* maximum may develop within, or just below the ice (Grainger 1977; Horner 1977), but biomass or production measurements of ice flora have never been made in Hudson Bay.

In summary from these considerations, it appears that during the summer months Hudson Bay is an oligotrophic body of water of low productivity, heavily influenced by freshwater runoff.

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Variability in the Diet of Ringed Seals, *Phoca hispida*, in Alaska

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LOWRY, L. F., K. J. FROST, AND J. J. BURNS. 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Can. J. Fish. Aquat. Sci. 37: 2254–2261.

Analysis of stomach contents of ringed seals (*Phoca hispida*) collected at eight locations along the Alaskan coast showed significant seasonal and regional differences in diet. During the spring–summer period saffron cod (*Eleginus gracilis*) was the most important food item in the nearshore zone of the northeastern Bering and southeastern Chukchi Seas. In that period shrimps (*Pandalus* spp., *Eualus* spp., *Lebbeus polaris*, and *Crangon septemspinosa*) were the major food in the northcentral Bering Sea, hyperiid amphipods (*Parathemisto libellula*) in the central Beaufort Sea and euphausiids (*Thysanoessa* spp.) in the boundary region (Barrow area) between the Chukchi and Beaufort seas. During late summer–early autumn hyperiid amphipods were important foods in the central Beaufort and the southeastern Chukchi. The autumn diet of seals in Norton Sound included mainly saffron cod During winter–early spring Arctic cod (*Boreogadus saida*) predominated the diet at all localities. During spring and early summer in the northeastern Bering and southeastern Chukchi seas the amount of saffron cod consumed was directly correlated with age. In the Beaufort Sea during autumn and winter Arctic cod were eaten in similar amounts by all age-classes. An analysis of the energy value and quantities of prey consumed indicates that prey species that occur in concentrations (Arctic and saffron cods, hyperiid amphipods, euphausiids and some shrimps) are of particular importance in the annual nutrition of ringed seals. These seals may be food limited in areas and during times when these kinds of prey are not available.

Key words: food habits, *Phoca hispida*, ringed seals, Arctic cod, saffron cod, crustaceans, Alaska

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Il existe des différences saisonnières et régionales marquées de régime alimentaire chez le phoque annelé (*Phoca hispida*), comme le démontre l'analyse des contenus stomacaux d'échantillons recueillis à huit endroits le long de la côte de l'Alaska. Dans la période printemps-été, la morue arctique (*Eleginus gracilis*) est l'aliment le plus important dans la zone littorale du nord-est de la mer de Béring et du sud-est de la mer de Tchouktche. À cette époque, les crevettes (*Pandalus* spp., *Eualus* spp., *Lebbeus polaris* et *Crangon septemspinosa*) constituent l'aliment principal dans le centre-nord de la mer de Béring, les amphipodes hypériides (*Parathemisto libellula*) dans le centre de la mer de Beaufort et les euphausides (*Thysanoessa* spp.) dans la région frontalière (région de Barrow) entre les mers de Tchouktche et de Beaufort. En fin d'été et début d'automne, les amphipodes hypériides sont des aliments importants dans le centre de la mer de Beaufort et le sud-est de la mer de Tchouktche. Dans la baie Norton, le régime automnal des phoques est constitué en grande partie par de la morue arctique. En hiver et au début du printemps, le saida (*Boreogadus saida*) prédomine dans le régime à tous les endroits. Au printemps et début de l'été, la quantité de morue arctique consommée est fonction directe de l'âge dans le nord-est de la mer de Béring et le sud-est de la mer de Tchouktche. Dans la mer de Beaufort, en automne et en hiver, le saida est mangé en quantités semblables par toutes les classes d'âge. D'après une analyse de la valeur énergétique et des quantités de proies consommées, les espèces proies qui se trouvent en concentrations (saida et morue arctique, amphipodes hypériides, euphausides et certaines crevettes) sont d'une importance particulière dans l'alimentation des phoques annelés. Ces phoques peuvent donc être limités par la nourriture dans les régions et aux périodes où ces proies ne sont pas disponibles.

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RINGED seals, *Phoca hispida*, are the most abundant and widely distributed phocids in the northern hemisphere (Scheffer 1958). They constitute the basic diet of polar bears, *Ursus maritimus* (Stirling 1974; Stirling and Archibald 1977) and are important to other predators, including Arctic foxes, *Alopex lagopus* (Smith 1976) and people. Many thousands are harvested annually by Inuit and other peoples of the Arctic Basin. These seals are a major trophic link in arctic and subarctic ecosystems.

The hunting of ringed seals in many parts of their

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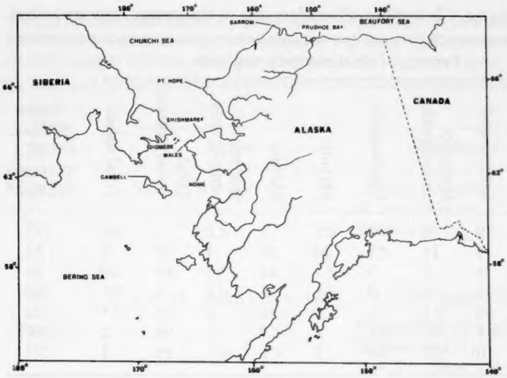

FIG. 1. Alaska showing locations of villages at which ringed seal stomachs were collected.

range has provided an opportunity to determine their food habits in several different areas. Published studies of their foods in Alaskan waters have all been limited in spatial and/or temporal coverage (Kenyon 1962; Johnson et al. 1966; Lowry et al. 1978). No previous studies have examined the possibility of age and sex-related dietary differences. In this paper we present additional information on the diet of ringed seals during various times of the year in seven widely separated locations. These results, when combined with those from previous studies, permit a more detailed overview and description of the food habits of these seals throughout much of their circumpolar range. Age and sex-related differences in food are examined. Some differences in foods are explained by distribution and movement patterns of major prey species. Also, the importance of various types of prey in the diet of these seals is evaluated on the basis of observed quantities consumed and estimated energy value of prey.

Materials and Methods

Most of the material examined in this study was obtained in northern Alaska from seals killed by Inuit subsistence hunters. We made additional collections at times and/or in areas where seals were not available to these shore-based hunters. Collections were made at seven locations (Fig. 1): two in the Bering Sea, two in Bering Strait, one in the Chukchi Sea, one at the convergence of the Chukchi and Beaufort seas and one in the central Beaufort Sea (approximately 80 km northwest of Prudhoe Bay). The date, local time, and, when possible, the exact location of collection were recorded for each seal examined.

A total of 973 stomachs which contained food were examined. After removal from the seals, stomachs were preserved by injection with and storage in 10% formalin, or by freezing. In the laboratory they were opened and the contents gently washed onto a 1.00-mm sieve and sorted macroscopically into major taxonomic groups. Items in these major groups were further identified and sorted to the lowest identifiable taxonomic level with the aid of appropriate keys and reference specimens. The volume of each invertebrate taxon was determined to the nearest 0.1 mL by water displacement in graduated cylinders. It was usually not practical to separate partially digested fish flesh and bones by species. Such material was combined for volumetric determination. The number of fish of each species (or higher taxon) in a stomach was determined on the basis of counts of recognizable whole fishes, otoliths, or diagnostic bones. A series of otoliths from each stomach usually was measured (maximum length to the nearest 0.1 mm) with vernier calipers.

The data from all seals obtained at a specific location during a designated time period were treated as a single sample. The volume of each invertebrate taxon as well as the volume of all invertebrate and all fish remains in stomachs comprising a sample were summed. These data were expressed as the percent of the total volume of contents in a sample comprised of a specific type of food. In a sample, the number of fish of each taxon occurring in each stomach was summed and expressed as a percent of the total number of all fishes. To determine the relative importance of fish and invertebrate taxa, a weighted value for each fish species (or group of related species) was calculated by multiplying the percent of the total number of each species of fish (or group of fishes) in a sample by the percent of total volume of all contents composed of fishes. In samples where more than one species of fish was a major food, the mean weight of individuals of each species was determined on the basis of the relationship of otolith length to fish length and fish length to weight of whole fishes (Frost and Lowry 1981). These values of mean weight of each fish species in a sample were then applied to the weighted values to derive adjusted values, which approximate the percent of the total food volume which was comprised of each species or group of fishes.

In August and September 1977, fishes were collected in 33 otter trawls made in the Beaufort Sea, including at least one trawl at each location where ringed seals were collected. The net used was a semi-balloon type with a 5.8-m headrope, 3.2-cm stretch mesh webbing and a 0.6-cm stretch mesh cod end liner. The net was towed on the bottom for 10 min at a speed of 5–7 km/h.

Results

The prey items of ringed seals in our samples were mainly of three general "types" and included: (1) fishes of the cod family (Gadidae); (2) pelagic nektonic crustaceans (those which swim in the water column); and (3) nektobenthonic crustaceans (those which are on or near the bottom.) For convenience, the latter two types are referred to as pelagic and benthic crustaceans. These food types were comprised of the following major taxa and species: gadid fishes include Arctic cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*); pelagic crustaceans include hyperiid amphipods (*Parathemisto libellula*) and euphausiids (*Thysanoessa* spp.); and benthic crustaceans include mysids (*Neomysis rayii* and *Mysis* spp.), shrimps (primarily *Pandalus* spp., *Eualus* spp., *Lebbeus polaris*, and *Crangon septemspinosa*), and gammarid amphipods (primarily *Anonyx nugax*, *Ampelisca* spp.,

TABLE 1. Food items of ringed seals, *Phoca hispida*, from the Bering, Chukchi, and Beaufort seas in the spring–summer period.

			Percent of total stomach contents										
Location	Dates	Sample size	Arctic cod	Saffron cod	Hyperiid amphipods	Euphausiids	Mysids	Shrimp	Gammarid amphipods	Total invertebrates	Total fishes	Mean volume of contents (mL)
Nome	June 1–26, 1977	13	<1	99	0	0	<1	1	<1	1	99	427
Gambell	June 1–15, 1977	25	1	1	11	<1	20	63	4	98	2	63
Diomede	May 27–June 3, 1977	7	38	1	1	0	<1	44	15	60	40	51
Wales	May 28–July 2, 1977	10	<1	91	0	0	<1	8	<1	9	91	269
Shishmaref	June 13–July 21, 1977	228	9	44	<1	3	3	31	2	43	57	99
Central Beaufort Sea	Sept. 1–2, 1977	13	2	<1	92	<1	4	<1	1	98	2	216
Barrow	Aug. 8–20, 1976	3	1	0	<1	96	1	<1	<1	99	1	271

and *Gammarus* spp.). In the following discussion prey type will refer to major ecological groups (e.g. benthic crustaceans) while kind of prey will refer to major taxa (e.g. shrimps).

In spring–summer collections at four locations a single kind of prey made up over 90% of the total volume of contents in the sample (Table 1). The dominant prey at Nome and Wales was saffron cod; near Barrow it was euphausiids; and in the central Beaufort Sea it was hyperiid amphipods. At three other locations no single kind of prey was overwhelmingly dominant. At Diomede and Shishmaref seals had eaten fishes and benthic crustaceans in approximately equal amounts. Crustaceans of several kinds made up most of the stomach contents of seals collected at Gambell.

Seasonal variation in ringed seal foods at four locations was examined for five time periods which generally correspond to major meteorological and sea ice events (Table 2). Gadid fishes were the major food type at Nome and Shishmaref in November to July. Benthic crustaceans were the most important foods at Point Hope in March to July and in the central Beaufort Sea in May–July. At two areas from which we have samples in the August to October period (Shishmaref and the central Beaufort Sea) pelagic crustaceans were the major food.

Potential differences in the diet of male and female ringed seals were examined using data from two areas (Table 3). Only seals 5 yr or more old were included in the analysis. At Shishmaref where large samples were collected, the proportions of the various kinds of prey in the diet were nearly identical in both sexes. In samples from the Bering Sea, female seals ate proportionally more saffron cod and less shrimps and gammarid amphipods than did males. However, the ranked order of importance of prey in the diet (saffron cod, shrimp, gammarid amphipods, Arctic cod) was similar for both sexes.

Age-related differences in food consumption were examined using data from seals collected in the spring–summer in the Bering Sea and southeastern Chukchi Sea (at Shishmaref), and in the autumn–winter period in the Beaufort Sea (Fig. 2). At Shishmaref stomachs of adult seals contained an average of about three times the quantity of food found in pups while in the Bering Sea adults contained more than seven times more. The mean quantity of invertebrates consumed by the various age categories ranged from 20 to 56 mL at Shishmaref and from 37 to 65 mL in the Bering Sea. The mean quantity of cod consumed by seals taken near Shishmaref increased from 18 mL in pups to 59 mL in seals 5 yr or more old. In the Bering Sea the corresponding increase was from less than 1 to 231 mL. In the Beaufort Sea a very different pattern was found. Arctic cod was the primary food for all age-classes and the amounts of the different prey types in the stomach increased little with age.

The quantity of each kind of prey required to fulfill the daily nutritional needs of ringed seals was calculated on the basis of calorific values of different prey

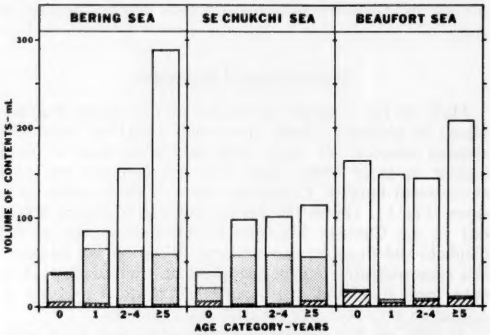

FIG. 2. Relationship between composition of stomach contents and age for ringed seals collected in three areas. Diagonal hatched area — pelagic crustaceans, stippled area — benthic crustaceans, white area — gadid fishes (saffron cod in the Bering Sea, Arctic cod in the Beaufort Sea, mostly saffron cod and some Arctic cod in the Chukchi Sea).

TABLE 2. Seasonal variation in foods of ringed seals at four locations. Numbers in parentheses are percent of total volume for invertebrate taxa and adjusted values for fish taxa, with the exception of data from Point Hope for which all values are percent of total sample volume. Only prey items contributing more than 5% of the total sample volume at one or more locality are listed.

Time period	Location			
	Nome	Shishmaref	Point Hope[a]	Central Beaufort Sea
May–July	Saffron cod (99)	Saffron cod (44) Shrimp (31) Arctic cod (9)	Shrimp (28) Mysids (16) Saffron cod (13) Amphipods (9) Arctic cod (7)	Gammarid amphipods (44) Shrimp (13) Arctic cod (10) Mysids (3)
	n = 13 mean vol = 427	n = 228 mean vol = 99	n = 329 mean vol = 46	n = 5 mean vol = 22
Aug.–Oct.		Hyperiid amphipods (88) Saffron cod (7)		Hyperiid amphipods (92)
		n = 6 mean vol = 122		n = 13 mean vol = 216
Nov.–Dec.	Saffron cod (56) Arctic cod (28) Sand lance (2) Shrimp (6)	Arctic cod (86) Saffron cod (14)	Arctic cod (49) Sculpins (23) Saffron cod (14) Amphipods (5)	Arctic cod (87) Hyperiid amphipods (12)
	n = 5 mean vol = 178	n = 7 mean vol = 273	n = 127 mean vol = 106	n = 19 mean vol = 168
Jan.–Feb.	Arctic cod (97) Saffron cod (3)	Arctic cod (83) Saffron cod (10)	Arctic cod (93) Shrimp (4)	Arctic cod (97) Euphausiids (2)
	n = 10 mean vol = 72	n = 24 mean vol = 315	n = 687 mean vol = 190	n = 24 mean vol = 248
Mar.–Apr.	Arctic cod (64) Shrimp (30) Saffron cod (3)		Shrimp (26) Amphipods (25) Arctic cod (16) Saffron cod (11)	Arctic cod (90) Hyperiid amphipods (6)
	n = 21 mean vol = 246		n = 287 mean vol = 93	n = 12 mean vol = 81

[a] Data from Johnson et al. (1966). Gammarid and hyperiid amphipods were not distinguished in the presentation of results.

(Tyler 1972; Atkinson and Wacasey 1976; Nishiyama 1977; Parsons 1977). Parsons (1977) estimated the caloric requirement of adult and pup ringed seals as 35 and 110 $\mathrm{kcal \cdot kg^{-1} \cdot d^{-1}}$ (1 kcal = 4.1868 kJ) respectively. Based on the weights of 761 known age ringed seals from Alaskan waters, we found the mean weight to be 13.9 kg for ringed seal pups and 46.1 kg for seals 5 yr or more old. The estimated daily caloric needs are therefore about 1529 kcal for pups and 1614 kcal for adults. A value of 1600 $\mathrm{kcal \cdot seal^{-1} \cdot d^{-1}}$ was used to estimate the quantity of each kind of prey needed to provide the daily caloric intake for both pups and adults. To facilitate comparisons of food requirements with volumes of stomach contents it was assumed that 1 kg of prey was equivalent to a volume of 1 L. The mean and maximum total volume of food in stomachs containing 50% or more of each of the seven major kinds of prey was determined (Table 4). The number of "stomachfulls" of a particular kind of prey required to satisfy the daily nutritional needs can be calculated by dividing the estimated daily food requirements by the recorded stomach contents volumes. Depending on the caloric value of the prey, an average seal requires about 1.1–2.8 L of food per day. The number of stomachfulls required to attain this volume on a daily basis varied greatly depending on the kind of prey consumed. If mean contents volumes are considered, all kinds of prey other than fishes would require more than 10 stomachfulls per day. Based on maximum volumes of stomach contents, a daily ration could be attained with less than five stomachfulls by pups only when they eat Arctic cod, and by adults when they eat Arctic cod, saffron cod, shrimps, hyperiid amphipods, or euphausiids.

Discussion

REGIONAL AND SEASONAL DIFFERENCES

Similar feeding patterns are evident in ringed seals from waters of northern Alaska, the northern seas of the USSR, northern Greenland, and near the Canadian Arctic islands (Table 5). Arctic cod are by far the major food during the months of November to April. These fish concentrate near shore to spawn during November to March (Andriyashev 1954). Beginning in April they apparently disperse into deeper water. Arctic cod were caught in 28 of 33 trawls we made in the Beaufort Sea in August and September 1977. However, although they were almost ubiquitous, the mean number caught per tow was only 5.9 (range

TABLE 3. Food items of male and female ringed seals collected near Shishmaref and in the Bering Sea.

	Shishmaref June–July 1976–1978		Bering Sea April–June 1975–1979	
Prey item	Females $n = 126$	Males $n = 100$	Females $n = 18$	Males $n = 14$
Arctic cod	8	5	2	1
Saffron cod	43	38	82	68
Hyperiid amphipods	<1	1	<1	<1
Euphausiids	1	3	0	0
Mysids	3	4	<1	<1
Shrimp	33	31	10	20
Gammarid amphipods	2	2	2	7
Total invertebrates	47	50	14	30
Total fishes	53	49	85	70
Mean volume of contents (mL)	111.1	120.7	340.0	221.9

0–26), indicating that they were widely distributed and not densely concentrated at that time. When the volume of Arctic cod eaten by ringed seals decreases in late spring and summer, benthic crustaceans become the most important food and the volume of food consumed decreases (Table 2). In late summer and early autumn pelagic crustaceans are the major food in offshore waters while mysids are commonly eaten in some nearshore areas. Generally, hyperiid amphipods are the primary kind of pelagic crustacean eaten in arctic waters while euphausiids are the primary food of seals from areas such as Barrow, Alaska and Ungava Bay, Canada, both of which are influenced by subarctic waters (Dunbar 1954 and 1957).

Ringed seals in the Sea of Okhotsk live under considerably different environmental circumstances than those in other regions. They do not bear their young on shorefast ice, but rather pup on the pack and spend summer and autumn in open water, occasionally hauling out on land (Fedoseev 1965). Euphausiids (associated with spring and summer periods of high productivity in the Okhotsk Sea) are their major foods and are eaten in large quantities during spring and summer. In the autumn and winter ringed seals in the Okhotsk Sea are presumed to feed in nearshore waters, utilizing a variety of boreal–subarctic fishes (Fedoseev 1965).

Ringed seals exhibit a seasonal feeding cycle which can be measured by changes in mean volume of stomach contents, the proportion of seals with empty stomachs and the average "fatness" of the seals in different seasons. Such changes were reported by McLaren (1958), Fedoseev (1965), and Johnson et al. (1966) and have been evident in our collections. In general, seals feed less frequently, catch less food, and become thinner during April to June. Based on our data on ringed seal weights, adult seals lose an average of 30 g/d from March to September and gain approximately 93 g/d in October and November. Most of this weight loss is in the form of blubber having a caloric value of about 9.5 kcal/g (Stirling and McEwan 1975). Assuming a daily metabolic requirement of 1613 kcal (35 kcal/kg for a 46.1 kg seal) the daily intake in the spring–summer period can be estimated as 1328 kcal while in the autumn, food intake must be approximately 2496 kcal. About 12 average stomachfulls of crustaceans would be required to supply the daily spring–summer caloric intake while the daily autumn intake would require about seven average stomachfulls of Arctic cod.

TABLE 4. Energy values of ringed seal prey, estimated quantity of each prey kind needed to satisfy daily caloric requirement, and total quantities of food found in stomachs containing ≥50% of each kind of prey.

			Total volume of food (mL) in stomachs containing ≥50% of specified kind of prey			
			Pups		Adults	
Kind of prey	Caloric value (kcal/kg[a] wet weight)	Estimated daily food requirements (mL)[b]	Mean	Maximum	Mean	Maximum
Arctic cod[c]	1408	1136	133	724	258	1200
Saffron cod[c]	1408	1136	46	215	232	1734
Hyperiid amphipods	625	2560	49	194	132	533
Euphausiids	665–1204	2406–1329	32	87	94	497
Mysids	990	1616	37	70	115	257
Shrimp	894–1320	1790–1212	38	124	121	630
Gammarid amphipods	565–699	2832–2289	41	143	106	284

[a] 1 kcal = 4.1868 kJ.

[b] See text for explanation.

[c] Based on energy value of walleye pollock (*Theragra chalcogramma*), from L. K. Miller, 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Final Rep. Marine Mammal Commission Contract No. MM5AC025.

TABLE 5. Summary of the major prey of ringed seals, *Phoca hispida*, in regions other than Alaska.

Region	Winter	Spring	Summer	Autumn	Source
Sea of Okhotsk	Saffron cod, smelt, herring, and other fishes	Primarily euphausiids, also gammarid and hyperiid amphipods and shrimps		Saffron cod, smelt, herring, and other fishes	Fedoseev (1965); Fedoseev and Bukhtiyarov (1972); Nikolaev and Skalkin (1975)
Bathurst Island			Mysids, hyperiid and gammarid amphipods		Finley (1978)[a]
Southwest Baffin Island, northern Foxe Basin	Hyperiid amphipods offshore; mysids, Arctic cod, and shrimps nearshore — no seasonality was found				McLaren (1958)
Ungava Bay and northern Labrador	Mysids, euphausiids, and fishes, including sand lance, pricklebacks, sculpins, and Arctic cod — no seasonality was found				McLaren (1958)
Baffin Island			Hyperiid amphipods and mysids		Dunbar (1941)
Northwest Greenland	Arctic cod, amphipods, and shrimps — seasonality not indicated				Vibe (1950)
Kara Sea, Novaya Zemlya	Arctic cod	Hyperiid and gammarid amphipods, and mysids		Arctic cod	Chapskii (1940)

[a] Finley, K. J. 1978. Behavior and densities of ringed seals (*Phoca hispida*) during haul out in the high Arctic, June 1977. Rep. prepared for Polar Gas Project by LGL Ltd., Toronto, Ont. 107 p.

SEX AND AGE-CLASS DIFFERENCES

No sex-related differences in diet were obvious in the samples of ringed seals we examined. However, age-related differences were in some instances dramatic. In the Bering Sea in spring saffron cod were eaten in large quantities by seals 5 yr or more old but in much smaller amounts by younger seals. Since our samples from the Bering Sea were collected at several locations over a 3-mo period, the results could be biased by the temporal and spatial distribution of collections of the various age categories. However, when collections at a single location were examined the pattern was similar to the Bering Sea as a whole. For example, 21 pups and yearlings taken at Wales in June 1977 and 1978 had a mean volume of contents of 50.1 mL, 97% of which was crustaceans. Seven seals 2 yr or more old taken at Wales in June had a mean contents volume of 369.4 mL, 94% of which was saffron cod. Saffron cod apparently were very abundant in the northern Bering Sea in spring but could be caught in large quantities only by older seals. At Shishmaref in June and July saffron cod were apparently less abundant than in the northern Bering based on volumes of food in adult seals. Therefore age-related dietary differences at Shishmaref were less dramatic. In the autumn–winter period in the Beaufort Sea there was little difference in the quantities and kinds of prey consumed by the different age categories. Arctic cod appear to be caught almost as easily by pups as by older seals. This difference is also indicated by the results shown in Table 4. In seals which had eaten mostly Arctic cod the mean volume of contents in adults was less than twice as great as that in pups. For seals which had eaten mostly saffron cod, adults contained more than five times as much food as did pups. Differences in saffron cod consumption in the Bering Sea cannot be simply attributed to the fact that pups in that sample had been recently weaned, since yearlings collected in the Bering Sea had also eaten only small volumes of saffron cod in comparison to older seals. The difference in suitability of arctic and saffron cods as foods for young seals is not at present explainable. Although saffron cod grow to a larger size than do Arctic cod the majority of both Arctic and saffron cod consumed ranged from 7 to 12 cm long regardless of age of the seal or area of collection.

SUITABILITY OF PREY

Based on the knowledge that ringed seals feed on a variety of organisms representing several trophic levels, McLaren (1958) concluded that "food is not likely a limiting factor in the local distribution and numbers of the seal." Interestingly, however, the mean volumes of stomach contents found in most of our samples were very small in relation to the estimated daily food requirements (Table 4). The relationship between the volume of contents in a stomach and the volume consumed by a seal during an "average" day (or longer period) is unknown. The mean and maximum volumes of food found in seals feeding on a particular prey type should reflect the ability of the seals to catch and consume that prey. Arctic and saffron cods appear to be particularly important foods since they are consumed in largest quantities. Arctic cod appear to be, by far, the best food for ringed seal pups. In comparisons of the mean volumes of prey, all types of crustaceans, which are taken in significantly lesser volumes than the gadids, appear to be relatively poor ringed seal forage. However, the maximum volumes found in adult seals consuming mostly hyperiids, euphausiids, and shrimps are large enough that the daily food requirement could be satisfied by two to five stomachfulls. Parsons (1977) found the digestive clearance rates for ringed seals to be 6–8 h, assuming intermittent feeding. This suggests that three to four feeding periods per day would be possible. Even with multiple daily feedings of maximum volume, mysids and gammarid amphipods appear to be inadequate for providing the energy needs of these seals. Seasonal changes in energy value of prey may affect our estimates of daily feeding requirements. For example, gadid fishes store energy in the form of oil in the liver and the energy content of whole fishes varies in relation to the liver index (Jensen 1979). Unfortunately, the only data we have on caloric value of Arctic cod deals with eviscerated fishes (Yudanov 1965). However, small variations in caloric value of prey would have little influence on our assessment of the relative value of different kinds of prey.

Seals, like all other animals, must consume enough food on an annual basis to maintain basic bodily functions. In addition, young animals devote a considerable amount of energy to growth while adults expend energy on reproduction. Several characteristics of ringed seal anatomy, distribution, and seasonal cycles seem to be adjusted to allow efficient utilization of seasonally available prey.

Throughout most of their range adult ringed seals occur at highest densities in regions of landfast ice in late winter to early summer (McLaren 1958; Burns 1970). This is often considered to result from a dependence on stable ice which provides an optimal platform for the care and weaning of young. We suggest that these concentrations of seals also depend on the abundant food resources made available by spawning Arctic and saffron cod. Breeding adult ringed seals are territorial (Stirling 1977) and may therefore exclude subadult seals from optimum foraging habitat. The importance of these abundant fishes, which can be caught by seals in large quantities, may be intensified by the fact that during this period of the year the seals are completing the accumulation of blubber reserves, growth of fetuses is occurring and significant amounts of time may be required for social activities such as birth lair formation and territorial defense. It is probably significant that Arctic cod do not occur in the Sea of Okhotsk (Andriyashev 1954) and this is the only region where shorefast ice is not the preferred pupping and breeding habitat of marine forms of ringed seals.

During late spring and early summer, ringed seals feed little and spend much time basking on the ice and molting. This period of reduced feeding occurs when available prey (primarily benthic crustaceans) appear to be difficult to catch in large quantities.

In late summer and autumn pelagic crustaceans are usually the primary food. Often several thousand euphausiids or hyperiid amphipods (mainly *Parathemisto* or *Thysanoessa*) are found in a single stomach. Fedoseev (1965) considered that the complex dentition of ringed seals allows them to capture such prey efficiently. To capture the numbers of these organisms found in stomachs, several must be captured in each mouthful and the water expelled through the small orifices between the occluded teeth. To be efficient, such feeding requires high densities of prey. Many species of zooplankton, including euphausiids and hyperiid amphipods, have patchy distributions. *Parathemisto* is known to form dense swarms during breeding (Gray and McHardy 1967). Dunbar (1957) noted that *P. libellula* began spawning in September. Large quantities of this species were found in ringed seals collected by Dunbar (1941) in August and September and by us in early September and late October. At that time of year the fatness and body weight of ringed seals rapidly increases. They spend most of their time in the water feeding, and apparently capture enough food to meet their daily food requirement and accumulate blubber.

The question of whether or not ringed seals are food limited remains unanswered, but it seems to be a real possibility. Certainly the ringed seal is adapted to exploit its potential food resources in the most efficient possible manner. Temporal and spatial differences in seal abundance during winter to early spring are probably related to differences in distribution of Arctic and saffron cods. Our observations suggest that in summer and early autumn seals are concentrated in areas where euphausiids or hyperiid amphipods are abundant. Similarly Chapskii (1940) has described a direct relationship between abundance of ringed seals and Arctic cod in some areas of the Siberian Arctic. On a longer time scale, differences in density, growth rates, and productivity of ringed seals in different parts of their range may be correlated with the abundance of Arctic cod and nektonic crustaceans. Year-to-year changes in abundance and productivity of seals, such as have been documented by Stirling et al. (1977) may similarly be explained by annular changes in prey abundance.

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Recurrence of Kills of Atlantic Herring (*Clupea harengus harengus*) Caused by Dinoflagellate Toxins Transferred Through Herbivorous Zooplankton

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WHITE, A. W. 1980. Recurrence of kills of Atlantic herring (*Clupea harengus harengus*) caused by dinoflagellate toxins transferred through herbivorous zooplankton. Can. J. Fish. Aquat. Sci. 37: 2262–2265.

Kills of adult herring occurred in two locations in the southwestern Bay of Fundy in July 1979 during a bloom of the toxic dinoflagellate *Gonyaulax excavata*. Fish showed the same symptoms as in a herring kill linked to *G. excavata* toxins in 1976. Herring stomachs contained *G. excavata* toxins (66–245 μg/100 g guts), the cladoceran *Evadne nordmanni*, and yellow-brown material probably of algal origin. At the time of the kills the zooplankton community was overwhelmingly dominated by *E. nordmanni*. Furthermore, bioassays showed the presence of *G. excavata* toxins in the zooplankters (18 μg/g wet plankton). Combined with evidence from the 1976 kill in which pteropods were vectors of the toxins, and with results from recent field and laboratory studies, these new observations and results substantiate that (1) *G. excavata* toxins can, and do, cause herring kills in nature with planktonic herbivores, *E. nordmanni* in this case, acting as vectors, and (2) the toxin transfer mechanism is a general phenomenon among herbivorous zooplankton. Similar food chain events may affect finfish in other areas of the world which experience blooms of toxic dinoflagellates.

Key words: dinoflagellate toxins, *Gonyaulax excavata*, herring kills, *Clupea harengus harengus*, cladoceran, *Evadne nordmanni*, red tides, zooplankton, fish kills

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Des mortalités de harengs adultes se sont produites dans le sud-ouest de la baie de Fundy en juillet 1979, au moment d'une floraison du dinoflagellé toxique *Gonyaulax excavata*. Les mêmes symptômes sont apparus chez les poissons que lors des mortalités de 1976, attribuées à *G. excavata*. Les estomacs de hareng contenaient des toxines de *G. excavata* (66–245 μg/100 g de tractus digestif), le cladocère *Evadne nordmanni* et un matériel brun-jaune probablement d'origine algale. À la même époque, la communauté zooplanctonique était complètement dominée par *E. nordmanni*. En outre, des essais biologiques démontrent la présence de toxines de *G. excavata* dans les zooplanctontes (18 μg/g de plancton humide). Ces observations nouvelles, combinées à la preuve obtenue en 1976 que les ptéropodes étaient vecteurs des toxines, de même qu'aux résultats d'études récentes sur le terrain et en laboratoire, démontrent que: (1) les toxines de *G. excavata* causent des mortalités de harengs dans la nature, les herbivores planctoniques, *E. nordmanni* dans ce cas, agissant comme vecteurs, et (2) le mécanisme de transfert des toxines est un phénomène général parmi le zooplancton herbivore. Des événements semblables se produisant dans la chaîne alimentaire peuvent affecter les poissons d'autres régions du monde où il y a des floraisons de dinoflagellés toxiques.

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ANNUAL blooms of toxic dinoflagellates occur along the Canadian Atlantic and Pacific coasts, contaminating shellfish with toxins and leading to the danger of paralytic shellfish poisoning (Prakash et al. 1971; Quayle 1969). Toxic blooms of *Gonyaulax excavata* (*tamarensis*) have a long history in the Bay of Fundy and in the St. Lawrence River Estuary. Since 1972 this organism has spread southward along the New England coast causing annual red tides as far south as Cape Cod (Anderson and Wall 1978).

In 1976 a herring kill in the Bay of Fundy was traced to *G. excavata* toxins which probably had been transmitted through the food chain to herring by the pteropod *Limacina retroversa* (White 1977). This was the first report implicating *G. excavata* in a fish kill in North America. It raised many questions regarding the generality of transmission of the toxins through planktonic

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herbivores, and the consequences to finfish.

More recent field and laboratory studies indicate that several herbivorous zooplankters are indeed capable of accumulating, and to some degree retaining, *G. excavata toxins* (White 1979, 1981). This supports the view that the toxins can be transmitted by herbivorous zooplankton and that this is a fairly general capability among these animals.

In 1979, herring kills caused by *G. excavata* toxins occurred again in the southwestern Bay of Fundy. This time the toxins were most likely transferred primarily through another planktonic herbivore, the cladoceran *Evadne nordmanni*. This paper summarizes these new events and discusses how they contribute to the confirmation of the *G. excavata* — herbivorous zooplankton — fish kill phenomenon.

Materials and Methods

Herring from the kill sites were collected as soon as possible after reports were received from fishermen. Fish from the Swallow Tail Light, Grand Manan, N.B. location (44°46′N, 66°44′W), most still alive and showing symptoms, were iced and brought to the laboratory within a few hours of the time of collection. Fish from the Moose Island, N.B. location (45°03′N, 66°46′W), dead and on the beach, were either brought uniced to the laboratory after a delay of several hours or were frozen for 2 d (in two different freezers) before being brought to the laboratory.

In the laboratory fish were weighed and measured, and stomach contents were examined immediately. Gut and muscle samples were homogenized in 0.1 N HCl within 1 d, and toxin extractions were completed within 2 d.

Amounts of paralytic, dinoflagellate toxins in gut, muscle, and zooplankton samples were determined using the standard mouse bioassay for shellfish investigations (AOAC 1975). Gut samples consisted of stomach, digestive cecae, and intestine plus their contents. Muscle samples consisted of strips of muscle tissue taken from near the gut cavity and from which most of the peritoneum was removed. Procedures for zooplankton samples have been reported previously (White 1979). Briefly, samples were ground in 0.1 N HCl, boiled, centrifuged, and extracts adjusted to pH 3.5 before being sent to the Department of Health and Welfare in Ottawa where bioassays using 10 mice per sample were conducted.

Toxicity values in this paper are reported in units of micrograms of saxitoxin (STX) equivalents because the bioassay is standardized with pure STX only.

Results and Discussion

On July 18, 1979, adult herring (16–27 cm) were reported acting strangely in the area of Swallow Tail Light, Grand Manan Island. Symptoms included loss of equilibrium, swimming on side or upside down, and gasping for breath. A similar observation was made in the same area on July 23. A small number of dead fish were reported in both instances.

On July 21, 1979, a kill of smaller herring (13–21 cm) was reported near Moose Island, New Brunswick. On that morning dead herring (estimated 20–25 t) were found at the bottom of a cove and washed up along the shore. The kill had occurred during the night, so behavioral symptoms were not observed.

All of these events occurred during the annual bloom of the toxic dinoflagellate *Gonyaulax excavata.* Plankton tows made regularly in the southwestern Bay of Fundy indicated that the *Gonyaulax* bloom reached its peak during the period of about July 13–16. However, a substantial number of *G. excavata* cells were still observed in surface waters on July 24.

Aside from *G. excavata*, the phytoplankton community during this period was comprised mainly of the ciliate photoautotroph *Mesodinium rubrum*, the dinoflagellate *Peridinium trochoideum*, and the diatom *Coscinodiscus asteromphalus.* Red tides caused by *M. rubrum* occurred in several locations in the southwestern Bay of Fundy in early July, and red water was, in fact, sighted in the Beaver Harbour–Blacks Harbour (Moose Island) area during the second week of July. Red tides of *M. rubrum* are nearly cosmopolitan and are not known to be directly toxic to fish (White et al. 1977). A mouse bioassay of *M. rubrum* extracts from 1979 red water showed no effect. Disintegration and decay of these red water organisms could, however, lead to oxygen stress in enclosed coastal areas.

The symptoms displayed by herring were the same as observed during the 1976 kill along the east coast of Grand Manan in which *G. excavata* toxins, probably transmitted by pteropods, were implicated (White 1977). These symptoms were also apparent in the laboratory when herring were orally injected with *G. excavata* toxins, in a study confirming the lethality of the toxins to herring (White 1977).

Results of the toxin assays for all herring gut samples tested in 1979 were positive, with levels ranging from 64 to 245 μg toxins per 100 g stomach, cecae, and intestine (Table 1). These amounts were considerably less than measured in the stomachs of adult herring during the 1976 kill (1414 μg toxins per 100 g). Even so, toxin levels were apparently sufficient to cause symptoms and some death of large herring near Swallow Tail and death of smaller herring near Moose Island. Since fish from the Moose Island area were decaying when sampled, the toxin assays may underestimate the actual levels that caused death.

Stomachs of herring from the Swallow Tail area contained little on both dates (Table 1). The dominant, nearly exclusive, zooplankton item was the cladoceran *Evadne nordmanni* in various stages of digestion. The more intact cladoceran specimens contained yellow-brown material consisting of chromatophore-like bodies, much the same as the material, verified to be of algal origin, found inside the ingested pteropods in the 1976 kill (White 1977). Also, as in 1976, this yellow to yellow-brown material was observed in the stomachs external to the ingested zooplankters. It is most likely, therefore, that this material consisted largely of the remains of *G. excavata* which had been eaten by the cladocerans. A few large centric diatoms

TABLE 1. Summary of data from herring kills in the Bay of Fundy in 1979 and 1976.

Location and date	No. of fish sampled	Mean (range) fork length (cm)	Mean (range) weight (g)	Stomach contents	Toxin content (μg/100 g)		Estimated toxin dose[c]		Remarks
					Gut[a]	Muscle	μg/fish	μg/kg body wt	
Swallow Tail, Grand Manan July 18, 1979	17	21.6 16–27)	110 (36–244)	Little total contents Contents dominated by *Evadne nordmanni* with yellow-brown material inside and out A few *Coscinodiscus asteromphalus*	110	<30[b]	5.9	54	Fish were still alive but showing symptoms — loss of equilibrium, swimming on side or upside down, and gasping for breath
Swallow Tail, Grand Manan July 23, 1979	17	21.8 (18–25)	116 (55–185)		245 (<30 for oil fraction)	<30	8.3	71	Same as above. These fish were iced without delay
Moose Island July 21, 1979	24	14.9 (12–21)	34 (16–72)	Little total contents Obvious decay with nothing recognizable except for small amount of whitish-yellow material	66	<30	0.8	23	Dead and decaying fish were collected from beach in the morning and either returned uniced to lab (*n* = 24) or placed in either of two freezers. Kill occurred during night so unsure of symptoms
Moose Island July 21, 1979	14	16.4 (15–18)	39 (27–58)		95	33	1.7	43	
Moose Island July 21, 1979	11	15.6 (13–17)	35 (27–47)		218	59	3.3	95	
Grand Manan, east coast July 15, 1976	40	21.5 (19–24)	~108 (~65–150)	Pteropods and yellow-brown, algal material inside and out (White 1977)	1414	<30	21.2	~197	Dead and dying fish displaying same symptoms as Swallow Tail fish above (White 1977)

[a] Includes stomach, digestive caecae, and intestine, except for 1976 sample which was for stomach only.
[b] 30 μg/100 g is the limit of detectability of toxin by the mouse bioassay.
[c] Based on toxin content of gut samples, mean gut weight per fish, and mean total weight per fish.

(*Coscinodiscus asteromphalus* up to 300 μm diam) were seen in the stomach contents, generally appearing extraordinarily intact.

Fish from the Moose Island area had decayed to the point at which little was recognizable in the stomachs except for a small amount of whitish-yellow, oozy material.

For the most part, toxins were undetectable in muscle tissue (Table 1), as was also the case in 1976. This is consistent with recent laboratory results indicating that herring killed by oral administration of *G. excavata* toxins show undetectable toxin levels in their muscle tissue (A. W. White unpublished data). These observations are consistent with the interpretation that the herring die when very small amounts of the toxins are absorbed through the gut. From this and because of the state of decay of the fish, it appears likely that the low toxin values in two of the muscle samples from the Moose Island fish are artifacts — probably a result of toxin leakage from the decaying gut and permeation into the surrounding muscle tissue.

That *E. nordmanni* was the dominant, nearly exclusive, item in the stomachs of Swallow Tail fish agrees with the composition of the zooplankton community during this period. Plankton tows made off Head Harbour, N.B., on July 24 showed that *E. nordmanni* overwhelmingly dominated the zooplankton community, accounting for more than 90% of the number of zooplankters caught by a 243-μm mesh net. Minor components were *Acartia clausii* and *Temora longicornis*. The enormity of the *E. nordmanni* population is demonstrated by the fact that a single, 10-min tow using a 1-m (diameter) net caught more than 2 kg (wet wt) of zooplankton. No pteropods were observed at this time nor had they been present for several weeks prior to the kills.

There is additional evidence indicating that *E. nordmanni* was the primary transfer agent of *Gonyaulax* toxins to herring in the 1979 kills. Toxin assays of the zooplankton material collected on July 24 gave a positive result of 18 μg toxins per gram wet weight of material. Because the sample was nearly all *E. nordmanni*, and because there were few, if any, free *Gonyaulax* cells in the sample, then the toxins must have been inside the cladocerans. Using the figure of 18 μg toxins/g and the estimated toxin dosages given in Table 1, the herring in the 1979 kills would have to have eaten only 0.04–0.46 g wet wt of zooplankton material to acquire the estimated toxin doses, which is feasible for fish weighing 34–116 g.

Results of other studies lend support to this interpretation as well. Toxins were also measured in zooplankton samples, in which *E. nordmanni* was abundant, during the 1977 and 1978 *G. excavata* blooms. Maximum toxin values were 59 μg/g wet plankton in both years (White 1979 and unpublished data). In addition, I have recently demonstrated in the laboratory that two herbivorous zooplankters, the copepod *Acartia clausii* and barnacle nauplii, can accumulate and retain the toxins when feeding on *G. excavata* (White 1981). Interestingly, in connection with the 1968 sand lance kill off the east coast of the United Kingdom which occurred during a *G. excavata* (*tamarensis*) bloom, the dominant zooplankter was also *E. nordmanni* (Adams et al. 1968). This fish kill prompted these authors to suggest that planktonic herbivores may have acted as vectors of the dinoflagellate toxins.

In summary, the evidence presented here, albeit largely circumstantial, points persuasively to the conclusions that the 1979 herring kills were caused by *G. excavata* toxins and that the cladoceran *E. nordmanni* was the primary vector of the toxins. Regarding the kill in the Moose Island area, disintegrating *M. rubrum* red water may, or may not, have been a contributing factor by causing localized oxygen stress.

When the information from these new events is combined with results of other recent studies which (1) implicate *G. excavata* toxins, probably transferred through pteropods, in a 1976 herring kill (White 1977), (2) demonstrate the lethality of the toxins to herring (White 1977), (3) show the presence of the toxins in natural zooplankton samples during *Gonyaulax* blooms (White 1979), and (4) establish the ability of two other zooplankters to accumulate and retain the toxins while feeding on *Gonyaulax* (White 1981), then this total body of knowledge leaves little doubt that *G. excavata* toxins can, and do, cause herring kills in nature, and that there is a rather general mechanism of transmission of these toxins by planktonic herbivores.

The Bay of Fundy will likely continue to experience recurrent herring kill episodes during *Gonyaulax* blooms. It is important to determine the significance of toxic dinoflagellate blooms and this toxin transfer mechanism by zooplankton for marine finfish in general, especially during their larval stages, not only in the Bay of Fundy, but in other areas of the world which experience frequent blooms of *G. excavata* or its relatives, particularly in New England, British Columbia, Gulf of Mexico, Japan, and northwestern Europe.

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Using *r-K* Selection Theory to Predict Natural Mortality[1]

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GUNDERSON, D. R. 1980. Using *r-K* selection theory to predict natural mortality. Can. J. Fish. Aquat. Sci. 37: 2266–2271.

Theory on *r-K* selection is used as a basis for examining correlations between instantaneous rate of natural mortality (M), gonad-body weight index, age at maturity, longevity, and Bertalanffy growth parameters (k, L_∞) for 10 species of marine fish. All correlations were consistent with *r-K* selection theory. The gonad-body weight index was found to be more highly correlated with M than any of the other life history parameters examined ($r^2 = 0.62$), and stepwise multiple regression showed that additional variables added little to the predictive ability of the model. The gonad-body weight index appears to be quite useful in predicting M, and development of an analogous index on an energetics basis might enhance its utility in this regard.

Key words: natural mortality, *r-K* selection, life history parameters

GUNDERSON, D. R. 1980. Using *r-K* selection theory to predict natural mortality. Can. J. Fish. Aquat. Sci. 37: 2266–2271.

La théorie de la sélection *r-K* a été utilisée comme base d'analyse des corrélations entre le taux instantané de mortalité naturelle (M), l'indice gonosomatique, l'âge de maturité, la longévité et les paramètres de croissance de Bertalanffy (k, L_∞) chez 10 espèces de poissons de mer. Toutes les corrélations sont conformes à la théorie de la sélection *r-K*. L'indice gonosomatique est relié plus étroitement à M que ne le sont tous les autres paramètres examinés du cycle biologique ($r^2 = 0{,}62$), et une régression multiple par étapes démontre que des variables supplémentaires n'ajoutent que peu à la capacité prévisionnelle du modèle. L'indice gonosomatique semble assez utile à prédire M, et un indice analogue, établi sur base énergétique, pourrait être encore plus utile sous ce rapport.

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ECOLOGICAL theory on r versus K selection has proven to be a useful tool in conceptualizing different extremes in life history strategy (Southwood 1976). The r (intrinsic rate of population growth) and K (carrying capacity of the environment) parameters from the logistic growth model $[(dN/dt = rN((K-N)/K)]$ are presumed to be subject to natural selection, so that different life history strategies evolve to adapt each species to its niche.

The r-strategists lie at one extreme, continually colonizing habitats of a temporary nature, with alternating "booms" and "busts" in population size. In this situation, natural selection will favor a short generation time, and allocation of available energy resources to reproductive activities. Since the habitats they colonize are often virtual ecological vacuums, high competitive ability is not required, and they will typically be small in size.

In contrast, K-strategists live in environments where mortality factors are relatively stable. Selection will favor a longer generation time, and allocation of available energy resources into enhancing survival through increased competitive ability, defensive mechanisms (e.g. spines, chemical defense), parental care, etc. Populations of these strategists will seldom depart substantially from long-term equilibrium levels. In actuality, a continuum of life history types exists between these extremes but it is reasonable to suppose that as body size, age at maturation, longevity, and commitment of available energy resources to gonadal development changes across this spectrum, there should be corresponding changes in the instantaneous rate of natural mortality (M).

The implications of *r-K* selection theory in the management of fish and marine mammal populations have been examined previously (Eberhardt and Siniff 1977; Estes 1979; Adams 1980), but the usefulness of this theory in predicting natural mortality rates has not yet been fully explored by fisheries workers. Beverton and Holt (1959) examined the utility of Bertalanffy growth parameters in predicting M, and found good correlations between k (the rate at which the asymptotic size, or L_∞, is approached) and M within the Clupeoidei, Gadiformes, Salmonoidei, and Pleuronectoidei. This correlation was less pronounced when species from dif-

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ferent taxonomic groupings were pooled, but still served to show a positive correlation between k and M. Both the Bertalanffy parameter k and intrinsic rate of population increase (r) are positively correlated with metabolic rate (Beverton and Holt 1959; Southwood 1976), and correlation between either of these parameters and M would be consistent with r-K selection theory.

Beverton (1963) enlarged on the previous analysis of clupeoids, and again found a positive correlation between k and M. He also found a positive correlation between the size at maturity and L_∞ (roughly equivalent to maximum body size), once again the result expected on the basis of r-K theory.

More recently, Jones and Johnston (1977) used a detailed model of the energy budgets for Arcto-Norwegian cod and North Sea haddock to estimate M, on the assumption that body size and age at maturity interact with natural mortality in such a way that the total reproductive output per individual is maximized. These assumptions correspond with those underlying r-K selection theory, and the range of values that Jones and Johnston obtained for M were generally consistent with previous estimates for Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*).

None of these workers have addressed r-K selection theory directly, however, and the purpose of this paper is to examine the utility of this theory in predicting natural mortality in fish populations. To do this, trends in natural mortality rate were evaluated in light of the features commonly used to distinguish r- and K-strategists in the ecological literature, i.e. longevity, age at maturity, maximum body size, metabolic rate, and proportion of body weight incorporated in reproductive organs.

Methods

PARAMETERS USED

Because a wide variety of information was required for the species used in this analysis, the field of candidates for inclusion narrowed rapidly. Reliable estimates of the instantaneous rate of natural mortality were most difficult to find, and data on gonad weight:body weight ratios were likewise somewhat limited. Determination of the latter parameter is difficult in the case of species which have a protracted spawning period or spawn several times a year, and only those species with a single, well-defined spawning season were used in this study.

If reliable estimates of M and gonad indices were available in the literature, the species in question had usually been studied intensively, and information on age at maturity, longevity, k, and L_∞ were also available. The data requirements were substantial, however, and eventually narrowed the number of species that could be employed to 10 commercially important marine species from temperate and boreal waters: North Sea plaice (*Pleuronectes platessa*), North Sea sole (*Solea solea*), Pacific halibut (*Hippoglossus stenolepis*), American plaice (*Hippoglossoides platessoides*), Atlantic cod (*Gadus morhua*), Pacific cod (*Gadus macrocephalus*), haddock (*Melanogrammus aeglefinus*), Pacific herring (*Clupea harengus pallasi*), Atlantic herring (*Clupea harengus harengus*), and capelin (*Mallotus villosus*). Two separate stocks of haddock, one from the Grand Banks and one from the North Sea, were included in the analysis.

All life history parameters (Table 1) were chosen so as to be as representative as possible of preexploitation conditions, and where data from a long-time series were available, the earliest reliable information was used. An attempt was also made to obtain information from a common geographical region to minimize variability caused by differences between stocks. Specific definitions of the parameters used in this model are as follows:

Instantaneous rate of natural mortality (M) — Most studies of fish populations have suggested that adult natural mortality is independent of fishing mortality, is relatively constant throughout much of the adult lifespan, then increases sharply once senescence begins. Cushing (1975) found it necessary to abandon use of a constant M for plaice older than age 15, and to employ a Gompertz equation[2] for 16–32-yr-olds. Beverton (1963) concluded that the increase in natural mortality with age was slight for most of the long-lived clupeoids, but became progressively sharper among the shorter-lived species. The age composition data for most of the species he studied could be described quite well by the Gompertz equation.

Obviously, the variability in M with age could cause significant problems in a comparative study such as this one if, for example, senescent individuals of one species were compared with juveniles of another. Fortunately, the estimates of M used in this study generally apply to the early adult age-groups, and this source of error is minimal. Sex-specific estimates of M frequently were not available, and values for the combined sexes were used in all comparisons.

Gonad index (GI) — This index was determined by dividing the gonad weight by body weight for females, and was used as a measure of the energy commitment that a given species had made toward the production of gametes. The index is superior to fecundity, or relative fecundity (fecundity per unit body weight) in this regard since it measures differences in both egg size and egg number. This is an important consideration, since egg size can vary substantially between species. Even within the Atlantic herring (*Clupea harengus harengus*) complex off Iceland, egg size is significantly smaller for summer spawners than for spring spawners. Liamin (1956) compared summer and spring spawners of the same size and maturity state and found that fecundity was 1.8–3.2 times higher in the former group, while gonad weight differences were negligible.

All gonad index data were obtained from information taken as closely as possible to the spawning season, using only those size- or age-groups that were fully mature (i.e. at least 90% of the individuals examined in that size/age-group were sexually mature). The gonad index for individual fish usually increases with size, so as many size-groups as possible were used to obtain the average for a given species.

In some cases, gonad index values were available directly from the literature (North Sea sole, capelin, Grand Banks

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[2] $N_t = N_o \exp - [\exp(m_o + m_1 t)]$ where m_o = natural mortality at the critical age (16 yr) and m_1 = rate at which senescent mortality increases with age.

TABLE 1. Life history parameters employed in this study, by species or stock.

	Species or stock											
	North Sea plaice		North Sea sole		American plaice		Pacific halibut		North Sea cod		Pacific cod	
Parameter	Value	Source	Value	Source	Value	Source	Value	Source	Value	Source	Value	Source
M	0.10	Beverton and Holt (1957)	0.10	De Veen (1976)	0.23	Pitt (1975)	0.19	IPHC Staff (1960)	0.20	Daan (1975)	0.91	Ketchen (1964)
GI	0.14	Simpson (1951)	0.11	De Veen (1976)	0.13	Pitt (1964)	0.12	Schmitt and Skud (1978)	0.10	Oosthuizen and Daan (1974), Daan (personal communication)	0.31	Westrheim (unpub.)
T_M (yr)	5	Hefford (1916)	3	De Veen (1976)	13	Pitt (1975)	12	Schmitt and Skud (1978)	4	Daan (1975)	3	Westrheim (1977)
$T_{0.01}$ (yr)	22	Cushing (1973)	14	ICES (1977a)	30	Pitt (1973)	23	IPHC Staff (1960)	10	ICES (1977b)	8	Ketchen (1964)
k	0.10	Beverton and Holt (1957)	0.39	De Veen (1976)	0.09	Pitt (1975)	0.13	Southward (1967)	0.30	Daan (1974)	0.27	Ketchen (1964)
L_∞ (cm)	68.50	Beverton and Holt (1957)	32.90	De Veen (1976)	59.40	Pitt (1975)	109.60	Southward (1967)	114.80	Daan (1974)	94.00	Ketchen (1964)

	Species or stock									
	North Sea haddock		Grand Banks haddock		North Sea herring		Pacific herring		Capelin	
Parameter	Value	Source	Value	Source	Value	Source	Value	Source	Value	Source
M	0.20	Beverton and Holt (1957)	0.20	Halliday (1971)	0.23	Cushing and Bridger (1966)	0.67	Tester (1955)	1.30	Beverton and Holt (1959)
GI	0.13	Raitt (1933)	0.12	Templeman et al. (1978a)	0.22	Hickling (1940)	0.19	Hay (unpublished data)	0.24	Prokhorov (1968)
T_M (yr)	3	Raitt (1933)	6	Templeman et al. (1978a)	4	Cushing (1968)	3	Taylor (1964)	3	Winters and Carscadden (1978)
$T_{0.01}$ (yr)	8	Blacker (1971)	12	Halliday (1971)	12	Gulland (1972)	10	Taylor (1964)	7	Winters and Carscadden (1978)
k	0.20	Jones (1962)	0.15	Templeman et al. (1978b)	0.38	Beverton and Holt (1959)	0.36	Trumble (1979)	0.48	Beverton and Holt (1959)
L_∞ (cm)	52.50	Jones (1962)	66.30	Templeman et al. (1978b)	30.00	Beverton and Holt (1959)	26.30	Trumble (1979)	19.50	Beverton and Holt (1959)

haddock, Pacific herring), or could be readily calculated from gonad weight and body weight data for individual fish (North Sea plaice, Downs herring, Pacific cod). For the remaining species, the mathematical relationships between different body parameters were used to obtain body weights and gonad weights for a representative series of size-groups, and the gonad index was then determined from the mean of these ratios. Length–fecundity, weight–fecundity, and ovary weight–fecundity relationships were used to determine the gonad indices for North Sea cod, American plaice, and Pacific halibut, while length–weight and length–ovary weight relationships were used for North Sea haddock.

Body weight was most frequently available on a dressed weight basis (i.e. "gutted weight" or "gutted and gilled weight"), and this measure was used for most species. Data on whole body weights were the only ones available for North Sea haddock, North Sea cod, Pacific herring, and capelin, however, resulting in gonad indices that are biased on the low side relative to the other species.

Age at maturity (T_m) — The youngest age at which 50% of the individuals examined are sexually mature is commonly used to characterize the maturation age for fishes, and was consequently used as the measure of T_m. In order to reduce variability due to between-sex difference in T_m, only the values obtained for females were employed wherever possible. The estimates for both Pacific herring and Downs herring are for both sexes combined, however.

Longevity ($T_{0.01}$) — The youngest age at which abundance had declined to 1% of the level present at T_m was used as the index of longevity. This parameter is less subject to variations in sample size than maximum reported age, and is also less sensitive to the effects of fishing. The age at maturity was chosen as a reference age because many species are not available to the commercial fishery until sexual maturity, and fisheries data were usually used to determine $T_{0.01}$. Age composition data frequently were not available by sex, and all estimates of $T_{0.01}$ were derived from data for the sexes combined to ensure consistency.

Bertalanffy growth parameters (k, L_∞) — The Bertalanffy growth model (Ricker 1975) has been widely applied by fisheries workers, and estimates of k and L_∞ were usually available from the literature. This was not the case for Pacific halibut, however, and estimates were obtained from a nonlinear least squares[3] fit of Southward's (1967) 1910–25 age–length data to the Bertalanffy model.

As with age composition data, estimates of k and L_∞ often were not available for each sex, and values for sexes combined were obtained for consistency. The estimates for American plaice were an exception to this practice, since k and L_∞ estimates were available only for females.

DATA ANALYSES

Stepwise multiple regression[4] was used to evaluate the relative effectiveness of GI, $T_{0.01}$, T_m, k, and L_∞ in predicting natural mortality (M). During each step in the procedure, the parameter that increased the multiple correlation coefficient (R^2) by the greatest margin was added to the model, and the process was continued until none of the remaining variables increased R^2 to a statistically significant degree.

Preliminary examination of the data showed that neither $T_{0.01}$, nor T_m were related to M in a linear fashion, and both variables were transformed (to $1/T_{0.01}$ and $1/T_m$, respectively) to remedy this. Untransformed values from Table 1 were used for all other variables.

Results

The signs of the correlation coefficients for the five life history parameters used in this study (Table 2) were all consistent with the results that would be predicted from *r-K* selection theory. Those species (or stocks) subject to the highest M tended to mature earlier, allocate a higher proportion of available resources to gonadal rather than somatic tissue, have higher indices of metabolic activity (k), and lower maximum body sizes (L_∞) than species with lower levels of natural mortality.

The strongest correlations were between M and *GI* (Fig. 1) and T_m and $T_{0.01}$, the latter correlation being analogous to the strong correlation that is often found between size at maturity and L_∞ (Beverton 1963). M might be forecast quite well from the gonad index for the species examined in this study ($R^2 = 0.62$), and an F test showed that the regression coefficient for GI in the equation, $M = 4.64\ \mathrm{GI} - 0.370$, was highly significant ($P = 0.004$).

The $T_{0.01}$ coefficient entered the model next ($M = 3.40\ \mathrm{GI} + 4.09\ T_{0.01} - 0.520$), and was statistically significant at the 0.15 level, but inclusion of this parameter reduced the standard error of the estimate only slightly (from 0.25 to 0.23). The single variable model is probably the best one to use in this situation, especially when the number of data points involved is taken into consideration.

The L_∞ parameter showed only weak correlation with M, *GI*, $T_{0.01}$, and T_m, and seemed to fit into the scheme of things rather poorly. This is not too surprising, however, since natural selection for maximum body size is influenced to a large degree by the size of the prey animals the adults depend on. An *r*-selected piscivore such as Pacific cod must grow to a substantial size if it is to exploit its resource base prop-

TABLE 2. Correlation coefficients (r) for natural mortality (M), gonad index (GI), longevity ($T_{0.01}$), age at maturity (T_m), and growth (L_∞, k) parameters in the 11 stocks examined in this study. Values in parentheses refer to transformed values of $T_{0.01}$ and T_m.

	M	GI	$T_{0.01}$	T_m	k
GI	0.79				
$T_{0.01}$	−0.50 (0.70)	−0.44			
T_m	−0.35 (0.49)	−0.38	0.87		
k	0.57	0.45	−0.70	−0.68	
L_∞	−0.29	−0.23	0.24	0.38	−0.56

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[3] SPSS program NONLINEAR, Northwestern Univ. Manual 433, 27 p. Vogelback Computing Center, 2129 Sheridan Road, Evanston, Il. 60201.

[4] SPSS program REGRESSION, Northwestern Univ. Manual 414 (Rev. B), 22 p. Vogelback Computing Center.

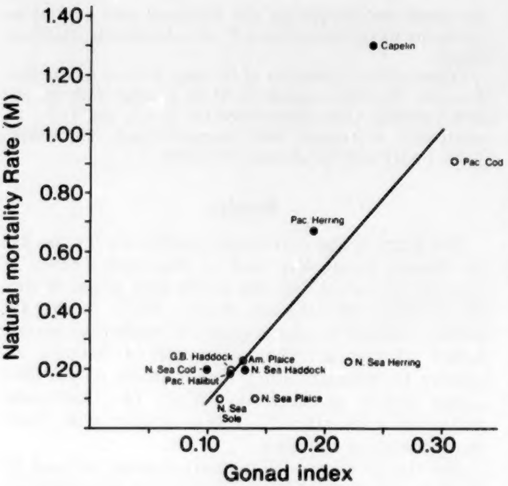

FIG. 1. Relationship between the gonad index (gonad weight ÷ body weight) and instantaneous rate of natural mortality (*M*) for the stocks examined in this study. Solid circles indicate species for which whole body weight was determined, empty circles denote dressed weight.

erly, even if its niche is a relatively unstable one. At the other extreme, the planktivorous food habits of the North Sea herring evidently place an upper limit on the body size it can attain, even though it appears to undergo relatively low levels of natural mortality.

Discussion

The results of this study suggest that *r-K* selection theory provides a useful basis for comparing life history strategies within marine fishes. Several problems were inherent in the analysis, notably the low sample size dictated by data availability, the low precision with which *M* was usually estimated, and the error introduced by using several different methods to determine the gonad index. A wide variety of life history types were examined, however, and the correlations between parameters employed to describe them were all consistent with *r-K* selection theory.

The correlation between the gonad index and natural mortality was particularly strong, and this relationship seems to characterize a species' location in the *r-K* selection continuum quite well. It appears that the gonad index can eventually be developed into a useful predictor of *M* for species whose commercial importance or geographic range is such that extensive research into their population dynamics cannot be carried out, or in cases where age determination is difficult.

A more systematic method of determining the relative allocation of available resources to gonadal tissue is desirable, however, and should be developed on an energy basis. Direct determination of the relative proportion of the energy budget that goes into the production of gonadal and somatic tissues over the course of a year would eliminate much of the variability associated with the gonad index used in this study, and would allow the scope of the investigation to be broadened considerably. The correlation between *M* and the reproductive:somatic energy ratio could be examined for tropical and subtropical species that spawn several times a year (e.g. sardines, anchovies, tunas) and for ovoviviparous or viviparous species (e.g. elasmobranchs and scorpaenids) as well as for the species dealt with in this paper.

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Use of a Multiplicative Model to Estimate Catch Rate and Effort from Commercial Data

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GAVARIS, S. 1980. Use of a multiplicative model to estimate catch rate and effort from commercial data. Can. J. Fish. Aquat. Sci. 37: 2272–2275.

The multiplicative model described by Robson can be used to obtain estimates of annual standardized catch rate and its variance by including years in the model. The corresponding estimate of standardized effort is the ratio of the total catch and the estimated catch rate. If the error is assumed to be lognormally distributed then these estimators have well defined statistical properties.

Key words: effort standardization, catch rate, multiplicative model, stock assessment

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Si l'on inclut les années dans le modèle multiplicateur décrit par Robson, on peut s'en servir pour obtenir des estimations du taux de capture normalisé annuel et de sa variance. L'estimation correspondante de l'effort normalisé est le rapport de la capture total et du taux de capture estimé. En supposant que l'erreur a une distribution log normale, ces estimateurs ont des propriétés statistiques bien définies.

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DATA from commercial fishery operations provides one of the most readily available sources of information which can be used to assess the condition of fish stocks. Two common uses of this data are surplus production models (Gulland 1977) and biomass indices (Ricker 1940).

For each species under study, the variables, catch, and effort, are generally measured according to country, gear type, tonnage class, month, and area fished. These classifications will be referred to as category types and their components as categories. For example February is a category in category type months. Catch rate is the ratio of catch and effort.

Both uses of commercial data mentioned above require a single value for total catch, total effort, and catch rate for each year (or other time unit). Various approaches have been used to obtain these series. The most direct method is to use the total effort applied by one type of gear multiplied by the ratio of its catch to the total catch to obtain total effort (Bishop and Wells 1978). Another approach is to estimate the relative fishing power of several prominent gear types with respect to a standard by performing regressions of each gear's catch rate against the standard. The effort of each gear type is then standardized when multiplied by its relative fishing power. The total effort is the sum of the standardized efforts multiplied by the ratio of their catch to the total catch (Parsons et al. 1976). A more sophisticated method is to estimate the relative power of several categories in any number of category types simultaneously (Robson 1966) and proceed as in the previous case. The annual catch rate would generally be computed by taking the ratio of total catch to total effort (Parsons et al. 1976).

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The properties of the estimators of catch rate and effort for the last two methods are not well defined. Furthermore computing these estimates is tedious for large data sets. In this paper a method to obtain an estimator of annual catch rate directly, using a multiplicative model like Robson's, is presented. An estimate of effort which is consistent with the catch rate may then be computed. Under the assumption that catch rate is a lognormally distributed variable the estimator of catch rate will be a minimum variance unbiased estimator and the estimator of effort will be unbiased. In addition a variance estimator and approximate confidence intervals for the estimator of catch rate are available.

The Model

One of the simplest, intuitively appealing models for relative fishing power, assuming that the catch of both categories is obtained from the same population, is

(1) $U_1 = U_2 P$

where

U_1 = catch rate of category 1
U_2 = catch rate of category 2
P = fishing power of category 1 relative to category 2

i.e. the catch rate of category 1 is directly proportional to the catch rate of category 2. An example of how this model has been used in stock assessments may be found in Parsons et al. (1976). The basic model can be extended by applying the principle of proportional effect to multiple categories in several category types. This would imply for example, that the catch rate in any month is a fixed proportion of the catch rate in another month. This model was most recently described by Robson (1966).

A general expression for such models would be

$$(2) \qquad U = U_R \prod_{ij} (P_{ij}{}^{X_{ij}})$$

where U = catch rate
U_R = catch rate for the particular combination of categories chosen as the reference (a single value)
P_{ij} = relative "power" of category j in category type i,

$$X_{ij} = \begin{cases} 1 \text{ when category } j \text{ occurs} \\ 0 \text{ otherwise} \end{cases}$$

The model states that any particular catch rate is equal to the product of the reference catch rate and "power" factors which take into account such things as country, gear type, area, etc. Further, no X variable or relative "power" coefficients are required for the reference categories. It should be noted that the terms reference and standard refer to different concepts.

Sissenwine and Bowman (1978) used this model to get estimates of the P's, the relative fishing power of two research vessels. For stock assessment the relative "powers" are not explicitly required. Rather, estimates of catch rate and effort which are comparable from year to year are needed.

By simply including years as a category type a series of annual catch rate is obtained if the other category types are kept fixed for some standard. Say, for example, that there was only one category type other than years and it contained four categories. If data was available for 3 yr then the specific model would be

$$U = U_R P_{11}{}^{X_{11}} P_{12}{}^{X_{12}} P_{13}{}^{X_{13}} P_{21}{}^{X_{21}} P_{22}{}^{X_{22}}$$

Note that one category from each category type is used as a reference. Suppose that category 2 of category type 1 is selected as the standard. A standardized annual catch rate series for the 3 yr is

$$U_0 = U_R P_{12}, \quad U_1 = U_R P_{12} P_{21}, \quad U_2 = U_R P_{12} P_{22}$$

which can be obtained by fixing the appropriate X's to either 0 or 1.

To get a standardized effort series the catch rate series is applied to the relationship

$$(3) \qquad E = C/U$$

where C = total catch in year k
E = effort that would have been expended by the standard to obtain the total catch

In order to consider the estimation problem some assumptions about the error structure must be made. The most straightforward model to use would be

$$(4) \qquad U = U_R \prod_{ij} (P_{ij}{}^{X_{ij}}) \exp(\epsilon)$$

where $\epsilon \sim N(0, \sigma^2)$ and $\rho(\epsilon_i, \epsilon_j) = 0,\ i \neq j$.

Then the corresponding model

$$(5) \qquad \ln \hat{U} = \ln U_R + \sum_{ij} [(\ln P_{ij}) X_{ij}] + \epsilon$$

may be solved using ordinary least squares. Specifically ln U, the natural log of the observed catch rate, is the dependent variable and the X's, the dummy variables specifying the categories, are the independent variables. To avoid linear dependence some linear constraints are required, in particular one linear constraint is needed for each category type. From the way the model is defined the constraints have been implicitly assumed to be $\ln P_i = 0$ for the reference category in each category type i. This is equivalent to $P_i = 1$, i.e. the relative "power" of the reference category in category type i is fixed as 1. The naive estimator for the mean catch rate

$$(6) \qquad \hat{U} = \exp(\widehat{\ln U})$$

where $\widehat{\ln U}$ = estimate for the mean of the ln catch rate obtained from the regression

will be biased. The minimum variance unbiased estimator for the mean catch rate and an unbiased estimator for the variance of this estimator are

$$(7) \qquad \hat{U} = \exp(\widehat{\ln U})\, g_m\left[\frac{m+1}{2m}(\hat{\sigma}^2 - \hat{\sigma}^2_{\widehat{\ln U}})\right]$$

$$(8) \qquad \hat{\sigma}^2_{\hat{U}} = \exp(2\,\widehat{\ln U})\left\{g^2{}_m\left[\frac{m+1}{2m}(\hat{\sigma}^2 - \hat{\sigma}^2_{\widehat{\ln U}})\right] - g_m\left[\frac{m+1}{m}(\hat{\sigma}^2 - 2\hat{\sigma}^2_{\widehat{\ln U}})\right]\right\}$$

(Bradu and Mundlak 1970)

where $\hat{\sigma}^2$ = the mean square residuals from the regression
$\hat{\sigma}^2_{\widehat{\ln U}}$ = estimate of the variance of $\widehat{\ln U}$ from the regression

$$g_m(t) = \sum_{p=0}^{\infty} \frac{mP(m+2p)}{m(m+2)\ldots(m+2p)}\left(\frac{m}{m+1}\right)^p \frac{t^p}{p!}.$$

$g_m{}^2(t) = (g_m(t))^2$
m = degrees of freedom for the residuals in the regression

Ebbeler (1973) has shown that, for computation, the following results may be used

$$(9) \qquad g_m(t) = \Gamma(m/2)\left\{m\left[\frac{-t}{2m+1}\right]^{1/2}\right\}^{1-(m/2)} J_{(m/2)-1}\left[m\left(\frac{-2t}{m+1}\right)\right]^{1/2} \quad \text{for } t < 0$$

$$(10) \qquad g_m(t) = \Gamma(m/2)\left\{m\left[\frac{-t}{2m+1}\right]^{1/2}\right\}^{1-(m/2)} I_{(m/2)-1}\left[m\left(\frac{2t}{m+1}\right)\right]^{1/2} \quad \text{for } t > 0$$

$$(11) \qquad \lim_{m\to\infty} g_m(t) = \exp(t) \quad \text{for all } t$$

where Γ is the Gamma function
J is the Bessel function of the first kind
I is the modified Bessel function of the first kind

In practice only equation 11 need be used since for $m > 50$ the approximation is very close.

Satisfactory approximate confidence intervals can be found using Cox's direct method (Land 1972).

$$(12) \quad \hat{\beta} = \widehat{\ln U} + 1/2\,\hat{\sigma}^2$$

$$(13) \quad \hat{\gamma}^2 = \hat{\sigma}^2_{\widehat{\ln U}} + \frac{1}{2(m+2)}\hat{\sigma}^4$$

then

$$(14) \quad \hat{U}_{\text{lower}} = \exp(\hat{\beta} - z_{\alpha/2}\hat{\gamma})$$

$$(15) \quad \hat{U}_{\text{upper}} = \exp(\hat{\beta} + z_{\alpha/2}\hat{\gamma})$$

where $\hat{\sigma}^4 = \frac{1}{m}\sum_i \epsilon_i{}^4$

α = confidence level
$z \sim N(0, 1)$

Using equation 3 and the result from equation 7 an estimator of total effort is

$$(16) \quad \hat{E} = C/\hat{U}$$

Estimates of ratios are generally biased but if the regression of the numerator on the denominator passes through the origin the estimator will be unbiased (Som 1973, p. 31). This estimator of effort will be unbiased since the regression of catch on catch rate must go through the origin.

Discussion

The first method referred to in the introduction requires that a particular category combination, the standard, be used from year to year. In situations where, for example, the standard gear type is absent for a year, or operated during a different season, this method cannot be applied. Furthermore, unless a large part of the catch is due to that particular category combination, a substantial amount of information may be overlooked.

These problems necessitate the use of a standardizing technique for many fisheries. Equations 7 and 11 provide a convenient method for estimating standardized catch rate series directly. The most important feature of the approach presented here is that the variance for the estimator of catch rate can be computed using equations 8 and 11 and inferences can be made using equations 12–15. As pointed out earlier both the standardized catch rate and the standardized effort, which is obtained by applying equation 16, have good statistical properties when catch rate is a lognormally distributed variable.

In applying this method all factors which could significantly affect catch rate would be included initially. If the conditional *F* in the analysis of variance shows that a category type is not significant then it can be removed from the final analysis. Category types need not be simple classifications. For example Gavaris (1980) used the composite country-gear type-tonnage class as a category type.

Removing a category type means that all the categories in that category type do not have significantly different regression coefficients i.e., ln relative "power," from each other. A less well defined problem which may arise is that some, but not all, coefficients are not different from each other. Some of the following methods may be used to help determine which coefficients to group together within each category type. The probability density functions of the coefficients can be graphed by using their estimated variances. Some form of multiple comparison test may be used (see, for example, Kramer 1957). A univariate cluster analysis may be performed on the regression coefficients. It should be kept in mind that the ultimate purpose of grouping is to reduce the mean square residuals and consequently the variance of the estimator of catch rate. Of course years would not be grouped if individual annual catch rates were required.

Although a coefficient may be found to be different in magnitude from others in its category type, it could be poorly determined due to variability in the data or lack of sufficient data. An indicator for this is the variance of the coefficient. It may be advantageous to exclude such categories and data from the final analysis since they do not add much information and may contribute disproportionately to the mean square residuals.

In practice, the amount of information that each data point contains is not equal. One catch rate may apply to 2 h of fishing by a small longliner whereas another may apply to 50 h of fishing by a large trawler. This situation can be handled by weighting. Some function of effort can be used to weight the points, but if efficiency of the different gears varies substantially a function of catch × effort may be better. After performing an unweighted regression the residuals may be plotted against catch × effort to help determine the form of the function (Draper and Smith 1966, p. 79).

The choice of a standard is arbitrary. Any standard will produce the same pattern in the catch rate series but some standards will have a smaller coefficient of variation. These will generally be the categories for which there is most information, i.e. the coefficients with small variance.

The model in its present form is best applied to the directed portion of a fishery. For some mixed fisheries the model would not apply. A solution to this important practical problem could be the basis of future research.

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Viral Erythrocytic Necrosis (VEN) in Atlantic Cod (*Gadus morhua*): In Vitro Studies

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RENO, P. W., AND B. L. NICHOLSON. 1980. Viral erythrocytic necrosis (VEN) in Atlantic cod (*Gadus morhua*): in vitro studies. Can. J. Fish. Aquat. Sci. 37: 2276–2281.

The effect of natural VEN infection on cod erythrocytes in vitro was studied using several methods. It was found that VEN-infected cells were more fragile in isotonic media than uninfected cells, but there was no difference in their susceptibility to hypotonic lysis. The proportion of VEN-infected cells was reduced in an inverse relationship to the time in culture. Incorporation of ^{3}H-labeled precursors into protein, RNA, and DNA occurred in both infected and uninfected cells during the first 6 d of incubation and declined thereafter. There was a greater incorporation of ^{3}H-amino acids and a tenfold greater incorporation of ^{3}H-thymidine into VEN-infected cells than in normal cells, while there was no difference in the incorporation of ^{3}H uridine by either type of cell. These results indicated that the virus of VEN was replicating in the erythrocytes and that the infection was detrimental to the cells.

Key words: viral erythrocytic necrosis, diseases, *Gadus morhua*

RENO, P. W., AND B. L. NICHOLSON. 1980. Viral erythrocytic necrosis (VEN) in Atlantic cod (*Gadus morhua*): in vitro studies. Can. J. Fish. Aquat. Sci. 37: 2276–2281.

Les auteurs ont étudié l'effet de la nécrose érythrocytaire virale (NEV). Ils constatent que les cellules infectées par la NEV sont plus fragiles en milieux isotoniques que les cellules non infectées, mais leur susceptibilité à la lyse hypotonique ne montre pas de différence. La proportion des cellules infectées par la NEV diminue en relation inverse du temps dans la culture. Dans les cellules infectées comme dans les non infectées, l'incorporation de précurseurs marqués à ^{3}H dans les protéines, l'ANR et l'ADN a lieu durant les 6 premiers jours d'incubation, pour décliner par la suite. L'incorporation de ^{3}H-acides aminés est plus poussée et celle de ^{3}H-thymidine est dix fois plus grande dans les cellules infectées par la NEV que dans les cellules normales. Par contre, l'incorporation de ^{3}H-uridine est la même dans l'un ou l'autre type de cellules. Ces résultats indiquent que le virus de la NEV s'auto-reproduit dans les érythrocytes et que l'infection cause des dommages aux cellules.

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RECENTLY, infections characterized by intracytoplasmic inclusions and nuclear changes in erythrocytes (E) have been reported in a number of poikilothermic vertebrates, including members of the classes Chondrichthyes (Johnston and Davies 1973), Osteichthyes (Evelyn and Traxler 1978; Laird and Bullock 1969; Sherburne 1973, 1977), Amphibia (Sherburne, personal communication), and Reptilia (Stehbens and Johnston 1966). Ultrastructural examination of the intraerythrocytic inclusions of several, but not all, species has revealed that hexagonal virus particles are present in the cytoplasm of affected cells. The viruses fall into three size classes characteristic of the host species infected: 140–190 nm in Atlantic herring (*Clupea harengus harengus*) (Reno et al. 1978), *Oncorhynchus* spp. (Evelyn and Traxler 1978), and American eel (*Anguilla rostrata*) (Doyle 1971); 200–250 nm in blenny *Blennius pholis* (Johnston and Davies 1973), gecko *Gephyra variegata* (Stehbens and Johnston 1966); and 300–350 nm in Atlantic cod (*Gadus morhua*) (Appy et al. 1976; Walker and Sherburne 1977).

In fishes, the infection was initially termed piscine erythrocytic necrosis by Laird and Bullock (1969), but the more general designation viral erythrocytic necrosis (VEN) suggested by Evelyn and Traxler (1978) will be used here.

Our efforts have been directed towards a characterization of VEN in cod; specifically, to assess the effect of VEN infection upon the host cell, the erythrocyte, and to determine if viral replication occurs in peripheral blood cells. Our experiments were performed in vitro to reduce the number of variables, and to avoid the problems engendered when marine fishes are held under laboratory conditions.

Our findings suggest that VEN virus replicates in cod E's, compromises the integrity of the erythrocyte in vitro, and alters cellular metabolism.

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Materials and Methods

FISH

Atlantic cod of 300–400 mm total length were collected from the Gulf of Maine, maintained for short periods in running seawater at the Maine Department of Marine Resources (West Boothbay Harbor, ME) then transferred to 2.5-m diameter pools where they were maintained in aerated synthetic seawater (Instant Ocean, Fisher Scientific, Medford, ME) at 12°C; fish were fed frozen shrimp or freshwater smelt.

MAINTENANCE OF E'S

Blood samples were collected by caudal venipuncture directly into marine PBS (MPBS) (NaCl, 0.188 mol/L; KCl 0.27 mmol/L; KH_2PO_4, 0.147 mmol/L; Na_2HPO_4, 0.5 mmol/L; pH 7.6) and washed three times in MPBS. The final pellet was resuspended in 5 or 10 vol of MPBS. Cod E's could be maintained for up to 2 wk with less than 50% lysis, as determined microscopically, when kept as static suspensions in MPBS at 4°C.

LYSIS EXPERIMENTS

The susceptibility of cod E's to lysis from VEN infection was determined by several methods.

To determine the fragility of E's in hypotonic conditions, one volume of packed cells was suspended in 10 vol of MPBS diluted in distilled water to various osmolarities and held at 4°C for 1 h. The intact cells were sedimented by centrifugation at 200 × *g* for 5 min, the absorbency of the released hemoglobin (Hb) was determined at 417 nm, and the percent lysis was calculated by comparison to a cell preparation lysed in distilled water.

The stability of VEN-infected E's under standard cultural conditions was determined by resuspending washed, packed E's in 10 vol of MPBS, incubating at 4°C and sampling at selected intervals. The absorbency of the Hb in solution was determined as described above, and percent lysis calculated.

To determine the fragility of VEN-infected cells in culture during an extended incubation, samples were taken daily for 12–14 d from cultures kept under standard conditions. Thin smears were fixed in methanol and stained with Giemsa stain (Fisher Scientific, Medford, MA). Five hundred to 1000 intact E's were counted and the percentage of E's showing VEN was calculated.

UPTAKE OF RADIOLABELED PRECURSORS

The incorporation of radioactive precursors into proteins and nucleic acids was determined in the following manner. An aliquot of packed E's was suspended in 10 vol of medium composed of MPBS, 5 μmol/L $MgCl_2$, 0.03 μmol/L each of adenosine, guanosine, and cytosine. A total of 1.85×10^8 Bq/mL of either ^{3}H-methylthymidine, ^{3}H-uridine, or an ^{3}H-amino acid mixture (New England Nuclear, Boston, MA) was added to each sample. The cells were incubated under standard conditions, and samples removed at intervals. Samples were washed free of extracellular label, then precipitated in trichloroacetic acid (TCA). The precipitates were washed twice in TCA, dissolved in 10 mL of an emulsifier-type scintillation fluid (Biofluor, New England Nuclear, Boston, MA), and counted in a scintillation counter. Concomitant with the samples for scintillation counting, samples of E's were counted to relate TCA-precipitable-cpm to a standard number of cells.

ELECTRON MICROSCOPY

Erythrocytes known to be VEN-infected were processed for electron microscopy after having been kept in culture for several days. Cells were washed with MPBS, prefixed for 1 h at 4°C in 2% glutaraldehyde, fixed in 1% OsO_4, dehydrated through a graded ethanol series and propylene oxide and embedded in Epon 812 (Pease 1964). Sections were cut, poststained with lead citrate and uranyl acetate, and examined in an EM201 (Phillips Instrument, Boston, MA) at an accelerating voltage of 60 kV.

BISBENZAMIDE STAINING

A modification of the procedure of Barile (1978) was used for specific histochemical staining of DNA, using a bisbenzamide fluorochrome stain (Hoechst #33258, Hoechst Pharmaceuticals, Somerville, NJ) at a concentration of 0.1 μg/mL of MPBS. Thin smears of cod E's were prepared, fixed in glacial acetic acid: methanol (1:3) for 5 min and air dried. The stain was applied at 23°C for 30 min and rinsed in distilled water. The smears were examined at 1000× on a fluorescent microscope with epi-illumination using a #50 barrier and BG12 exciter filters.

Results

SUSCEPTIBILITY TO HYPOTONIC LYSIS

When erythrocytes from VEN-infected and normal cod were held in hypotonic solutions, there was no appreciable lysis until the suspending medium reached a tonicity of 210 mOsm (Fig. 1). Below this tonicity, lysis occurred rapidly; there was, however, no measurable difference between the fragility of VEN-infected and normal E's.

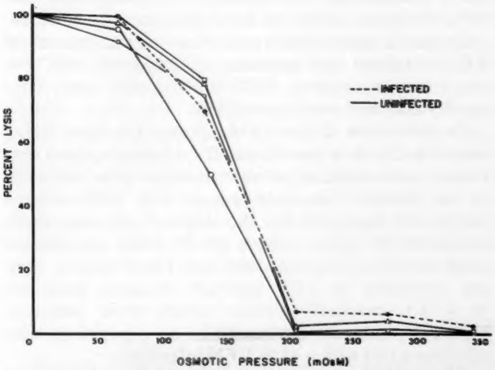

FIG. 1. Susceptibility of erythrocytes of VEN-infected and normal cod to hypotonic lysis. The dashed line represents E's from VEN-infected cod; the solid lines represent cells from normal fish.

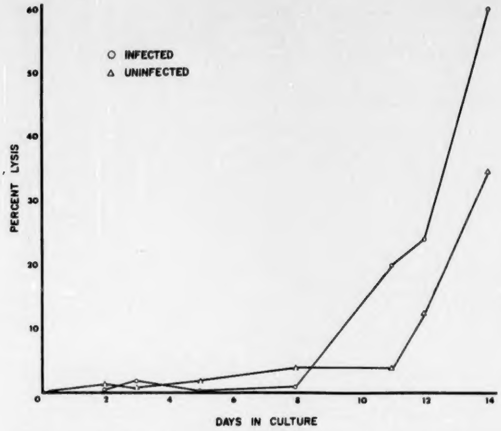

FIG. 2. Effect of length of maintenance in culture on lysis of erythrocytes from VEN-infected (○) and normal (△) cod. Lines represent mean values for three trials.

IN VITRO LYSIS

The fragility of VEN-infected E's in culture was examined by two methods. A suspension of E's containing VEN-infected cells was tested by absorbency measurements at a wavelength of 417 nm (Fig. 2). During the first 8 d in culture there was no difference between the rate of lysis of VEN-infected and uninfected cell suspensions; however, by day 11, cells in the VEN-infected suspension had begun to lyse at a higher rate than did the E's from normal fish. The final level of lysis after 14 d was 60 and 38% in infected and uninfected cultures, respectively. In this case, the increased lysis in the VEN-infected cell suspension amounted to 22%, while only about 12% of the E's appeared VEN-infected by microscopic observation at the outset of the experiment; in other experiments a similar difference between the percent of VEN infection and amount of enhanced lysis was noted, but in all cases, VEN-infected cells lysed more readily than cells from normal fish.

To determine if the VEN-infected E's were lysing more rapidly than uninfected E's, Giemsa-stained thin smears were prepared at various times after initiation of the culture. Preliminary results with VEN-infected herring E's suggested that the infected cells were more susceptible to lysis in culture (P. W. Reno unpublished results). In several trials with cod E's exhibiting various intensities of VEN infection (ranging from 1.6 to 45%), markedly similar results were obtained. Figure 3 represents the results of an experiment with E's from a cod with a 45% VEN infection.

When a smear was prepared from whole blood the sample contained 45% VEN-infected E's. After the cells had been washed free of serum components and clotting factors and resuspended in MPBS, however, this value fell to approximately 33%. Consequently, at day 0, about one-third of the E's were VEN-infected. During the 11-d incubation period, a significant linear decline in the VEN-infection rate was observed, from about 33% to about 17% (least squares methods $P < 0.001$). In two other experiments, with blood from other VEN-infected cod, the % of VEN-infected E's went from 1.6 to 0.2% and from 3.1 to 0% over a 12-d period, with the decline in each instance inversely proportional to the time in culture.

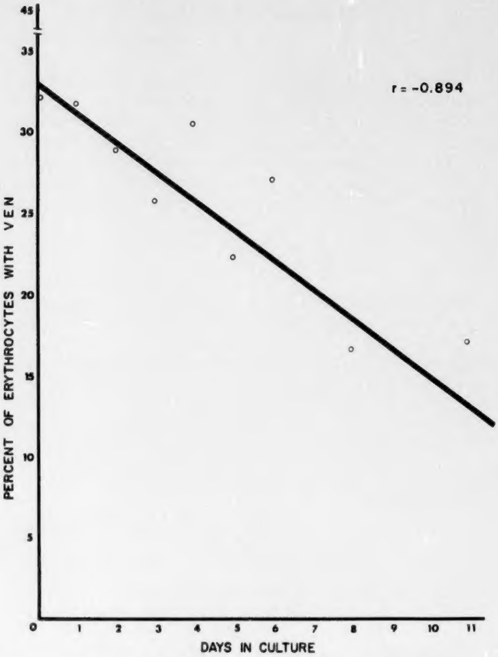

FIG. 3. Effect of length of maintenance in culture on proportion of VEN-infected cells present.

UPTAKE OF RADIOLABELED PRECURSORS

The incorporation of ^{3}H-labeled precursors into macromolecules was determined for both VEN-infected and uninfected E's. In these experiments the percent of VEN-infected E's was 10–20%.

Incorporation of tritiated amino acids into protein began to occur rapidly in both VEN-infected and uninfected cells and continued without any discernible differences until day 5 (Fig. 4). On day 6 the amount of ^{3}H incorporated by VEN-infected cells had reached a level twice that of the uninfected cells; both declined thereafter to a similar level after a 13-d incubation.

There was a slow, but significant rate of incorporation of ^{3}H-uridine into RNA of both infected and un-

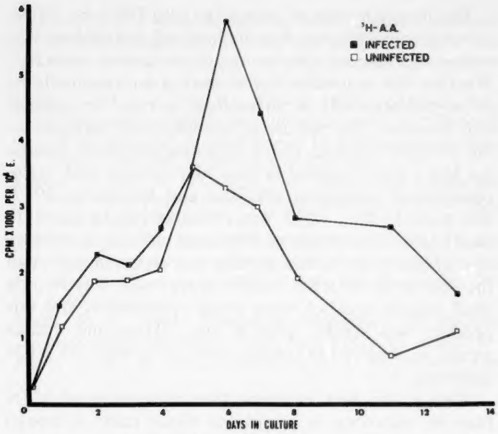

FIG. 4. Incorporation of ^{3}H-amino acids into erythrocytes of VEN-infected (■) and normal (□) cod during in vitro maintenance.

infected cells for the first 6 d, after which the rate leveled off or began to decline somewhat (Fig. 5). There was no difference between the rates of incorporation of ^{3}H-uridine into RNA of VEN-infected or uninfected cells, however.

There was no appreciable incorporation of ^{3}H-thymidine into DNA by E's from normal cod (Fig. 6). In contrast, the incorporation of ^{3}H-thymidine increased almost 5-fold for VEN-infected E's during the first day in culture. The level then continued to rise for 5 more d, when almost a 10-fold difference in the amount of thymidine was incorporated by VEN-infected cells. Again, there was a marked decline in the amount of thymidine incorporated after 6 d in culture, but the level in VEN-infected E's remained relatively high. In four other trials comparable results were obtained.

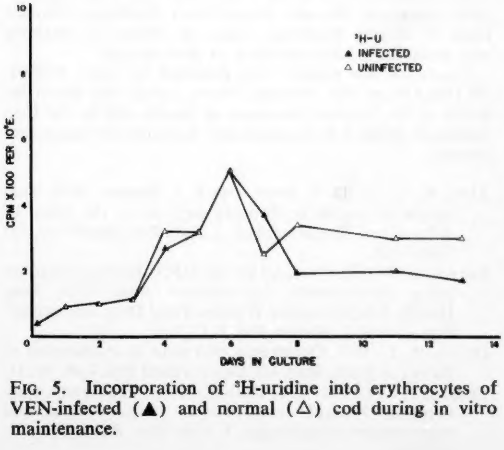

FIG. 5. Incorporation of ^{3}H-uridine into erythrocytes of VEN-infected (▲) and normal (△) cod during in vitro maintenance.

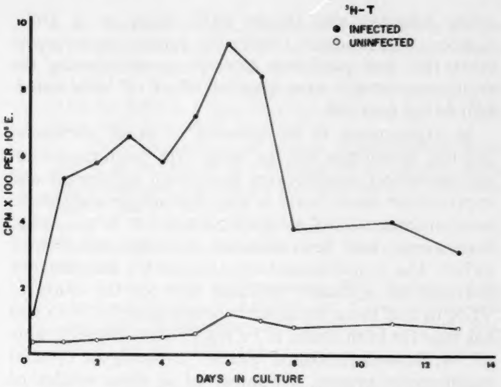

FIG. 6. Incorporation of ^{3}H-thymidine into erythrocytes of VEN-infected (●) and normal (○) cod during in vitro maintenance.

BISBENZAMIDE STAINING

The results of the DNA-specific bisbenzamide stain showed that the nuclei of all cells stained an apple green, and in addition, VEN-positive cells show clearly delineated fluorescing cytoplasmic inclusions, identical in size and shape to those seen in Giemsa stained specimens. The proportion of cells exhibiting this specific cytoplasmic fluorescence was identical to that obtained by Giemsa staining.

ELECTRON MICROSCOPY

To determine if maintaining E's in vitro altered the morphology of VEN virus or the infected cells which were infected, ultrathin sections of Epon-embedded E's were made and examined in the electron microscope.

VEN-infected cells taken either directly from the fish or from a culture maintained in vitro under the previously mentioned conditions showed no differences in ultrastructure. In both cases the virion was composed of several electron-dense and translucent layers, with the outer capsid exhibiting a marked hexagonal profile. The virions ranged from 300–350 nm in diameter edge-to-edge and were surrounded by an amorphous light-staining region; many VEN-infected cells under both conditions showed evidence of a viroplasm.

Discussion

Investigations of VEN thus far have been primarily of a descriptive nature, documenting the presence of a viral agent in the E's of numerous poikilothermic vertebrates (Appy et al. 1976; Evelyn and Traxler

1978; Johnston and Davies 1973; Reno et al. 1978; Stehbens and Johnston 1966). The present report represents the first published attempt at elucidating the replication of the virus and the effect of VEN infection on the host cell.

In experiments to be reported in detail elsewhere, cultural conditions for the long-term maintenance of marine teleost erythrocytes have been delineated and approximate those found in vivo. Previously, only short-term maintenance of teleost E, limited to hours rather than weeks, had been initiated (Greany and Powers 1978). The establishment of extended E's maintenance provided an especially valuable tool for the study of VEN in cod since intraspecific transfer of VEN in cod has thus far been found to be feasible but unpredictable (P. W. Reno unpublished results). Utilizing the optimal maintenance system, a number of in vitro studies of VEN were undertaken.

The results of the in vitro lysis experiments (Fig. 2 and 3) provided firm evidence that VEN infection can cause necrosis of E's. While the lysis of VEN-infected E's in vitro cannot be strictly correlated to a similar situation in vivo, there have been reports that VEN infection in salmonid species results in anemia (Evelyn and Traxler 1978; MacMillan and Mulcahy 1979). In cod, however, there was no difference in hematocrits between normal and VEN-infected fish (S. W. Sherburne personal communication), nor were there any disease signs evident in adult fish. This does not indicate that VEN infection in cod may not have untoward consequences, however. Since the dynamics of hematopoiesis in cod and other teleosts remains uncharted it is possible that even if VEN-infected cells become necrotic, the organism may be able to replenish even an extensive loss of E's rapidly enough to ameliorate the deficiency before it is noted. The absence of a detectable effect of VEN infection on hematocrit may be due to the extensive variance of the hematocrits of both VEN-free and VEN-infected cod — a range of about 30% (S. W. Sherburne personal communication).

In culture, VEN-infected cells lysed more rapidly than did normal cells (Fig. 3) indicating that in the in vitro system used here, they were more fragile than normal E's. The linear nature of the decline in the proportion of VEN-infected cells was evidence that the lesion responsible for lysis occurred immediately rather than after a lag period. Similarly, the lesions responsible for the overall enhancement of lysis of cultures containing VEN-infected E's (Fig. 2) could not be entirely accounted for on a microscopic level and were probably due to subcellular biochemical alterations. Several attempts at infecting cod E's in vitro have been unsuccessful (P. W. Reno unpublished results), thus minimizing the possibility that this enhanced lysis is due to direct cell-to-cell transfer of VEN. Normal E's are quite sensitive to microenvironmental changes and the burden of virus infection may be sufficient to promote lysis; the results of the radiolabel incorporation studies are one indicator of biochemical alterations of E metabolism caused by VEN infection.

The incorporation of thymidine into DNA by VEN-infected cells indicates that the host cell metabolism was redirected toward producing viral-induced material. Whether this induction was occurring intranuclearly or intracytoplasmically is unresolved. It must be pointed out, however, that the use of histochemical methods — the Feulgen reaction and a bisbenzamide stain specific for DNA have resulted in positive reactions with intracytoplasmic inclusions (Walker and Sherburne 1977; this paper); thus, DNA was probably incorporated directly into viral progeny. The concomitant incorporation of amino acids into protein was expected, although the low level of RNA synthesis was not. But if only viral specific m-RNA were being synthesized, and this product was stable, little if any, ^{3}H-uridine uptake would be observed in cultures with a low intensity VEN infection.

This is the first evidence that replication of VEN may be occurring in peripheral blood cells. Although only mature E's show evidence of VEN infection in cod, it may be that the viral maturation process may occur in E precursors such as reticulocytes or normoblasts, or even earlier at some stem cell stage. We have found that by electron microscopy only cells which appear to be fully mature — that is, lacking evidence of mitochondria, Golgi complex, or endoplasmic reticulum — contain evidence of VEN infection. Consequently, VEN infection may induce the E, primarily a vehicle for oxygen transfer, to expand its functional capacities beyond its normal limits and cause cell destruction.

The experiments undertaken here are only a first step toward understanding the events during VEN infection. They must be followed by more biochemically oriented work to permit greater understanding of the virus-cell interaction.

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Crustacean Zooplankton Communities of Acidic, Metal-Contaminated Lakes Near Sudbury, Ontario

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YAN, N. D., AND R. STRUS. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37: 2282–2293.

Crustacean zooplankton data for 1973 to 1978 from Clearwater Lake, an acidic, metal-contaminated lake near Sudbury, Ontario, are presented and compared with data from four other contaminated lakes near Sudbury and six uncontaminated lakes in the Muskoka–Haliburton Region of Ontario. Species richness and community biomass were reduced in the contaminated lakes, the latter because of reductions in numbers and average size of community dominants. The greatest reductions were observed in the lake with the highest metal levels, Hannah Lake. Cladocera were much more important contributors to total biomass in the contaminated lakes, forming, for example, 80–96% of the average biomass for the ice-free period in Clearwater Lake. An average of 89% of all adult crustacea observed in Clearwater Lake were *Bosmina longirostris* (O. F. Müller). Zooplankton biomass in the contaminated lakes, excluding Hannah Lake, was not significantly correlated with pH, with Cu, Ni, or TP concentrations, or with total phytoplankton biomass. While similarities existed, community structure was different from that of acidic lakes in the La Cloche Mountains that were not contaminated with Cu or Ni. Hypotheses relating to how acidification alters typical phytoplankton–zooplankton interactions were constructed. The scarcity of quantitative data required to test such hypotheses is emphasized.

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L'article qui suit présente des données sur le zooplancton crustacé recueilli de 1973 à 1978 dans le lac Clearwater, un lac à caractère acide contaminé par des métaux dans le voisinage de Sudbury, en Ontario, et les compare avec des données de quatre autres lacs contaminés de la région de Sudbury et de six lacs non contaminés de la région de Muskoka–Haliburton de l'Ontario. La diversité des espèces et la biomasse des communautés sont réduites dans les lacs contaminés, cette dernière par suite de la diminution du nombre et de la taille moyenne des espèces dominantes des communautés. Les plus fortes diminutions se rencontrent dans le lac où les concentrations de métaux sont maximales, le lac Hannah. Dans les lacs contaminés, les cladocères fournissent les apports de beaucoup les plus importants à la biomasse totale. Ils constituent, par exemple, 80 à 96% de la biomasse moyenne dans le lac Clearwater pendant la période d'absence de glace. *Bosmina longirostris* (O. F. Müller) constitue en moyenne 89% de tous les crustacés adultes observés dans le lac Clearwater. Il n'y a pas de corrélation significative entre la biomasse zooplanctonique dans les lacs contaminés, à l'exclusion du lac Hannah, et le pH, les concentrations de Cu, Ni ou PT, ou encore la biomasse phytoplanctonique totale. Bien qu'il existe des analogies, la structure des communautés diffère de celle des lacs à caractère acide des montagnes La Cloche non contaminés par Cu ou Ni. Des hypothèses sont mises de l'avant sur la façon dont l'acidification altère les interactions phytoplancton–zooplancton typiques. On fait ressortir la rareté des données quantitatives requises pour vérifier ces hypothèses.

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STUDIES conducted in different parts of the world have demonstrated that although the biomasses of phytoplankton communities of lakes acidified by the atmospheric deposition of strong acids are no lower than those of nonacidic lakes with similar concentrations of phosphorus, the structure of the communities of acidic lakes is quite different from that of nonacidic lakes (Almer et al. 1978). Recently, several regional surveys of the zooplankton of acidic lakes have been conducted. While these have demonstrated that the diversity of zooplankton communities is reduced by acidification (Hendrey et al. 1976; Almer et al. 1978; Leivestad et al. 1976) and that point-in-time community structure of acidic and nonacidic lakes differs (Sprules 1975), the available information on the seasonal variability (Roff and Kwiatkowski 1977; Janicki and DeCosta 1979) and the biomass (Bible 1972) of zooplankton populations in acidic lakes is unfortunately very limited. Studies designed to investigate the inter-

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action of phytoplankton and zooplankton communities in acidic lakes have not been performed, although it is known that herbivorous zooplankton can directly affect the standing stock and structure of phytoplankton communities (Shapiro 1978; Andersson et al. 1978; Hrbácek et al. 1961). Therefore, it cannot yet be ascertained if the changes in the phytoplankton communities that do occur in acidic lakes might, to any extent, be attributable to changes in zooplankton communities.

Lakes near Sudbury, Ontario, that are acidic and contaminated with heavy metals have been investigated for many years (Gorham and Gordon 1960; Beamish and Harvey 1972; Dillon et al. 1979). Phytoplankton in these lakes have adapted to conditions of low pH and high Cu and Ni concentrations (Stokes 1975) but at concentrations of Cu and Ni of about 100 and 300 μg L^{-1}, respectively, the structure of phytoplankton communities is determined by pH, not by metal toxicity (Yan 1979). Sprules (1975) and Roff and Kwiatkowski (1977) have documented some changes in zooplankton communities accompanying acidification of La Cloche Mountain Lakes about 65 km southwest of Sudbury that do not have elevated Cu and Ni levels. It is not known whether the contamination with Cu and Ni of acidic lakes closer to Sudbury produces additional changes in zooplankton communities. As both Cu and Ni are toxic to zooplankton (Biesinger and Christensen 1972) at levels frequently lower than those recorded in Sudbury lakes (Dillon et al. 1979) and as the susceptibility of zooplankton to metals varies tremendously among species (Baudouin and Scoppa 1974) such changes should be anticipated.

Since 1973, we have been studying Clearwater Lake and three other lakes (Middle, Hannah, and Lohi) that have been acidic (pH 4.1–4.6) and contaminated with Cu and Ni for between 20 and 80 yr. We have studied Nelson Lake, a lake at an earlier stage of acidification (pH $\simeq$5.6), since 1975. While the chemistry of the latter four lakes has been manipulated by experimental additions of neutralizing or fertilizing substances (summarized in Dillon et al. 1979) we have not adjusted the chemistry of Clearwater Lake. Since 1976 we have also been studying six lakes with low alkalinities in the Muskoka–Haliburton Region of south-central Ontario. Six years of zooplankton data from Clearwater Lake are presented in this paper and compared with premanipulation data from the other acidic lakes, with premanipulation and postmanipulation data from Nelson Lake (manipulation of lake pH did not influence the zooplankton of this lake, Yan et al. [1977]), and with data from the other nonacidic lakes. The objectives of this study are:

1) To describe seasonal and annual variations in the biomass and community composition of the crustacean zooplankton community of Clearwater Lake.

2) To construct preliminary hypotheses concerning ways in which acidification of lakes influences typical interactions between phytoplankton and zooplankton at the community level.

Materials and Methods

Scheider et al. (1975) and Yan (1979) have described the methods employed for the collection and analysis of chemical and phytoplankton samples, respectively.

From 1973 to 1975, zooplankton in Clearwater, Middle, Lohi, and Hannah lakes were collected with an unmetred, Wisconsin net (11 cm diameter, 80-μm mesh) which was towed vertically from 1 m above the sediment surface to the surface at the deepest location in each lake. From 1976 and onward, samples were taken using a 34-L, self-closing, plastic trap (Schindler 1969) at 2- to 3-m intervals to 1 m above the sediment surface in the Sudbury and Haliburton lakes. Except for a short period in 1977 in which 40-μm mesh was used in Clearwater Lake, the trap's attached net and bucket was equipped with 80-μm mesh. Trap samples were taken at four stations in the Sudbury lakes (collections from the same depths from different stations were subsequently combined) and at the deepest location only in the Haliburton lakes. All samples were preserved in the field with a neutralized, sugar-formalin solution (Haney and Hall 1973). Sampling periods are indicated in Table 1.

In the laboratory, trap samples were transferred to graduated cylinders, made up to 100 mL with tap water and mixed by bubbling with air. A fraction of each sample proportional to the volume of the lake stratum from which the sample had been taken was removed with a wide-mouth pipette. These fractions were pooled to provide a single morphometrically weighted sample presumed to be representative of the whole lake.

The monographs routinely used to identify zooplankton were those of Edmondson (1959) and Brooks (1959). No attempt was made to identify nauplii. Copepodids were identified to suborder. All crustacean zooplankters were enumerated if the sample contained <200 individuals; otherwise at least 200 individuals were enumerated.

The mean annual biomass of all dominant zooplankters was determined for each lake. To do this 50–300 individuals (depending on their size) were chosen to equally represent all size-classes observed in a year. These were removed from the samples, rinsed four times with distilled water to remove adhering preservative, placed on preweighed coverslips, dried to constant weight ($\simeq$24 h) at 80°C and weighed to the nearest microgram on a Sartorius electrobalance. Separate dry weights were obtained for naupliar, copepodid, and adult copepods.

Counts of dominant zooplankters in each lake in each year were converted to biomass using the measured weights (Table 2). Where possible, individual weights of less common species were taken from other years or other study lakes. Because they were not sufficiently common to measure weights in our study lakes, the mean dry weight of *Epischura lacustris* was taken from Thompson Lake (R. Strus unpublished data) and weights of *Simocephalus* sp., *Ceriodaphnia megalops*, and *Polyphemus pediculus* were obtained from other collections (J. Cooley, Department of Fisheries and Oceans, Burlington, Ont., personal communication).

Ice-free period averages of biomass or community composition were corrected for any differences in sampling frequency by generating monthly averages and averaging the monthly means.

Description of the Study Area

The location and selected aspects of the morphometry

TABLE 1. Latitude, longitude, lake surface area (A_0), mean depth ($\bar{z}$), and dates for which zooplankton data are reported (sampling period) for the study lakes.

Lake	Latitude (°N)	Longitude (°W)	A_0 (ha)	$\bar{z}$ (m)	Sampling period[a]
Clearwater	46°22′	81°03′	77	8.1	Aug.–Nov. 1973 May–Oct. (Nov.) 1974–1978
Hannah	46°26′	81°02′	27	4.0	Aug.–Nov. 1973 May–Nov. 1974
Lohi	46°23′	81°06′	41	6.2	Aug.–Nov. 1973
Middle	46°23′	81°06′	28	6.2	July–Nov. 1973
Nelson	46°44′	81°05′	309	11.6	May–Oct. 1975, 1976
Blue Chalk	45°12′	78°56′	49	8.5	May–Nov. 1977
Red Chalk	45°11′	78°56′	57	14.2	May–Nov. 1977
Harp	45°23′	79°08′	67	12.4	May–Nov. 1977
Jerry	45°23′	79°06′	50	12.4	May–Nov. 1977
Chub	45°13′	78°59′	32	8.9	May–Nov. 1977
Dickie	45°09′	79°05′	93	5.0	May–Nov. 1977

[a] Clearwater, Hannah, Lohi, Middle, and Nelson lakes were sampled biweekly. The remaining lakes were sampled weekly.

TABLE 2. Weights used in conversion of counts to biomass for common species in the acidic lakes (Middle, Hannah, Lohi, and Clearwater), Nelson Lake and the other nonacidic lakes. Weights of less common species are available from the authors on request.

	Dry weight (μg animal^{-1})		
	Acidic lakes	Nelson Lake	Other nonacidic lakes
Copepoda			
Nauplii	0.37[a]	0.37	0.11
Cyclopoid copepodid	0.78[b]	1.75	1.50
Cyclops vernalis	3.14[b]	—	3.14[b]
C. scutifer	—	5.74	6.42
C. bicuspidatus thomasi	—	4.60	3.24
Tropocyclops prasinus mexicanus	—	0.87	0.47
Mesocyclops edax	—	10.7	6.46
Calanoid copepodid	1.17[c]	1.17[c]	0.87
Diaptomus minutus	2.0[a]	2.0	2.24
D. oregonensis	—	—	3.55
Epischura lacustris	—	—	15.9
Cladocera			
Daphnia galeata mendotae	—	—	8.76
D. dubia	—	—	4.50
D. retrocurva	—	—	3.14
D. pulex	—	—	8.09
Bosmina longirostris	0.74[b]	0.78	0.54
Holopedium gibberum	—	—	10.94
Diaphanosoma leuchtenbergianum	—	—	1.89
Chydorus sphaericus	0.59[b]	—	0.90
Ceriodaphnia megalops	2.0[d]	—	0.50

[a] From Nelson Lake collections.
[b] From Clearwater Lake collections.
[c] From Schindler and Novén (1971).
[d] By comparison with weighed species with similar dimensions.

of the study lakes are summarized in Table 1. Dillon et al. (1979) have summarized the chemistry of Clearwater, Middle, Lohi, and Hannah lakes. The chemistry, phytoplankton, and experimental manipulations of Nelson Lake are summarized by Yan et al. (1977). Selected aspects (pH, SO_4, Al, Mn, alkalinity) of the chemistry of the Haliburton Lakes have been previously tabulated (Dillon et al. 1978; Scheider et al. 1979). Yan (1979) and Nicholls (in preparation) summarized phytoplankton data for the study lakes.

The study lakes are all clear (annual mean Secchi depths 6–11 m in the Sudbury lakes and 3–7 m for the Haliburton lakes). Temperature regimes are related to lake morphometry and transparency. Blue Chalk, Red Chalk, Harp, Jerry, Chub, and Nelson lakes are first-class dimictic lakes. Dickie, Clearwater, Lohi, and Middle lakes are second-class dimictic lakes, and Hannah Lake, the shallowest of the lakes is third-class dimictic (definitions after Hutchinson 1957).

All except Dickie Lake are oligotrophic (0.5–3.0 μg chlor *a* L^{-1} for the Sudbury lakes and 2.0–6.0 μg chlor *a* L^{-1} for the Haliburton lakes). Total N:Total P ratios are generally 20–50 by weight indicating that phosphorus is the nutrient present in shortest supply (Schindler 1977).

Unusually large atmospheric loadings of heavy metals (Jeffries and Snyder 1980) have resulted in elevated concentrations of Cu and Ni in the Sudbury lakes. Substitution of H^+ from precipitation for cations in the overburden of the watersheds during runoff has resulted in elevated levels of Ca, Mg, Al, and Mn (Dillon et al. 1979). Al and Mn concentrations are elevated in other acidic lakes in Ontario more remote from Sudbury (Beamish and Van Loon 1977; Scheider et al. 1979). Elevated levels of Cu and Ni exist only in lakes within about 70 km of Sudbury (Dillon et al. 1979).

The Sudbury study lakes that are acidic have been so for at least two decades. While the Haliburton lakes are not acidic, their buffering capacities are very low and precipitation in the area is very acidic (Dillon et al. 1978). In consequence, the pH's of surface water of the lakes with

TABLE 3. Comparison of selected crustacean zooplankton data from net (1973–75) and trap (1976–78) collections from Clearwater Lake. To be comparable with 1973 data, data from August onward were used for 1974–78. Averages are reported except where otherwise indicated.

	Net			Trap		
Parameters	1973	1974	1975	1976	1977	1978
Numbers						
No. of species collection^{-1}	3.6	4.1	4.0	3.5	4.3	3.7
No. of organisms L^{-1}	7	25	4	14	24	15
Maximum No. of adults L^{-1}	21	39	4	28	54	26
No. of *B. longirostris* (% of adults)	96	99	99	99	99	97
Biomass						
Total crustacea (mg m^{-3})	5.0	19.2	3.3	11.2	17.1	9.4
Cladocera (% of crustacea)	90	98	78	90	98	94
B. longirostris (% of crustacea)	89	97	77	89	96	87

the lowest alkalinities (Chub and Dickie) are depressed to 5.0 for a short time in early spring (Jeffries et al. 1979).

All of the study lakes are situated in the Precambrian Shield, an area that in terms of crustacean zooplankton communities may be considered a single zoogeographic region (Patalas 1971; Sprules 1975). Within this region, Patalas (1971) identified four community types related to lake morphometry. All of the study lakes except Nelson Lake fall within Patalas' Type II category, those of intermediate size and depth. Nelson Lake fits the larger and deeper Type I category. Both these categories, however, are characterized by zooplankton communities dominated by *Cyclops bicuspidatus thomasi* and *Diaptomus minutus* (Patalas 1971).

Results

NET VS. TRAP COLLECTIONS

Several investigators have demonstrated that data derived from unmetred townets underestimate standing stocks of crustacean zooplankton, especially those of species with more highly developed avoidance mechanisms (Schindler 1969; Pederson et al. 1976). When data from trap and net collections from Clearwater Lake were compared (Table 3), no significant bias ($P > 0.01$, one-way ANOVA with sampling gear as treatments, yearly averaged data as observations) attributable to sampling gear was detected for any of the parameters which were compared. In Clearwater Lake there were large variations in standing stocks even among years when the same sampling devices were employed (Table 3). These differences undoubtedly overshadowed any differences attributable to sampling gear.

NONACIDIC LAKES

The Muskoka–Haliburton lakes together with Nelson Lake were considered the "nonacidic" lakes, as Sprules (1975) and Yan et al. (1977) demonstrated that zooplankton communities of lakes in the Sudbury area retained their integrity until their pH dropped below 5.7, the most acidic pH of these study lakes.

Zooplankton communities of the Haliburton Lakes will be described in detail elsewhere. Selected summary data only are presented herein.

An average of between 7 and 15 species were identified in each sample in the nonacidic lakes. Total crustacean biomass varied between 26 and 86 mg m^{-3} with copepods contributing an average of 65% (36–96) of the total (Table 4). The biomass and relative contributions of Cladocera and Copepoda to the biomass were within the same order of magnitude as those of nonacidic, oligotrophic lakes in northwestern Ontario, the USA, and Italy for which data could be averaged over the ice-free period (Table 4).

When expressed as densities (numbers of individuals L^{-1}) rather than as biomass, the importance of Copepoda was more evident. The total density varied from 18.2 to 45.5 animals L^{-1} (Table 4). Excluding nauplii, a mean of 85% (71–93) of the animals recorded were Copepoda (Table 5). Assuming that all calanoid copepodids were immature forms of *D. minutus*, an assumption which probably only slightly exagggerated its importance, *D. minutus* formed between 44 and 73% of all crustacean zooplankton, and was dominant (>10% of total density) in all lakes (Table 5).

Cyclopoid copepods contributed 10–37% of the total density, copepodids usually of *Cyclops bicuspidatus thomasi*, *C. scutifer*, and *Tropocyclops prasinus mexicanus* being most important. Cladocera formed 6–30% of the total density. *Bosmina longirostris* was dominant in Nelson and Harp lakes and *Holopedium gibberum* in Harp and Dickie lakes. *Daphnia galeata mendotae* and *Diaphanosoma leuchtenbergianum* were commonly important but they were not dominant when data were averaged over the ice-free period, in any of the lakes (Table 5).

ACIDIC LAKES

Seventy-nine zooplankton samples from Clearwater Lake were examined. These had an average of only 3.7 species per sample indicating that species richness was much less than in the nonacidic lakes (Table 4). Ninety percent of the collections had between three and five species, suggesting that the average number of species that exist at any time in acidic lakes may be accurately estimated from a small number of samples. The average number of species per collection observed in Middle and Lohi lakes was quite comparable to that of Clearwater Lake, but somewhat fewer species were identified in each sample in Hannah Lake, the lake with the highest metal levels (Table 4).

Thirteen species of crustacean zooplankton were identified in Clearwater Lake collections. Four were observed once only, and only three (*B. longirostris*, *Chydorus sphaericus*, and *Cyclops vernalis*) were present in all years (Table 6). *Bosmina longirostris* was dominant in all samples. *Cyclops vernalis* was often codominant in the early spring. In comparison with

TABLE 4. A summary of selected chemical and zooplankton data from the study lakes. Data from other lakes are presented for comparison. Values are averaged for the ice-free period unless otherwise stated.

Lake	Source	Collection method	pH	[TP] µg L⁻¹	[Cu] µg L⁻¹	[Ni] µg L⁻¹	No. of species collection⁻¹	No. of animals L⁻¹	Crustacean biomass: Total mg m⁻³	% Crustacea: Copepoda	% Crustacea: *B. longirostris*	% Crustacea: Other Cladocera	Lake type
					Acidic study lakes								
Clearwater 1973	This study	Net	4.3	6	98	280	3.6	7.1	5.0	10	89	1	Oligo.
1974	This study	Net	4.2	6	101	290	3.4	17.3	13.2	4	95	1	Oligo.
1975	This study	Net	4.3	4	100	270	3.9	6.1	4.3	12	87	1	Oligo.
1976	This study	34L trap	4.2	5	91	270	3.5	12.4	8.6	19	81	<1	Oligo.
1977	This study	34L trap	4.1	7	81	280	3.9	18.7	13.8	6	93	1	Oligo.
1978	This study	34L trap	4.4	5	74	260	3.6	9.8	6.5	20	79	1	Oligo.
Hannah 1973	This study	Net	4.3	8	1090	1620	2.9	1.1	0.68	29	60	11	Oligo.
1974	This study	Net	4.3	6	1110	1870	3.1	0.64	0.71	58	35	7	Oligo.
Middle 1973	This study	Net	4.4	7	496	1060	3.4	19.7	13.7	8	92	<1	Oligo.
Lohi 1973	This study	Net	4.4	6	84	250	3.6	36.0	24.0	19	81	<1	Oligo.
					Nonacidic study lakes								
Nelson 1975	This study	34L trap	5.7	5	22	16	8.0	36.5	34.0	96	2	2	Oligo.
1976	This study	34L trap	6.5	5	13	10	7.0	32.6	35.1	84	14	2	Oligo.
Blue Chalk 1977	This study	34L trap	6.6	8	<2	<2	11.9	43.0	48.8	64	0.3	35.7	Oligo.
Red Chalk 1977	This study	34L trap	6.4	6	<2	<2	14.6	28.9	31.0	69	0.6	30.4	Oligo.
Harp 1977	This study	34L trap	6.4	8	<2	<2	12.5	18.2	31.5	44	3.0	53.0	Oligo.
Jerry 1977	This study	34L trap	6.4	10	<2	<2	9.3	23.8	26.0	79	0.3	20.7	Oligo.
Chub 1977	This study	34L trap	5.7	10	<2	<2	11.0	45.5	48.6	75	0.1	24.9	Oligo.
Dickie 1977	This study	34L trap	6.0	13	<2	<2	10.3	36.4	85.7	36	0.06	64	Oligo/meso
					Other lakes								
122	Schindler and Novén (1971)	29L trap	6.5[a]	13, 3[b]	—	—	8[c]	—	81	61		39[d]	Oligo/meso
132	Schindler and Novén (1971)	29L trap	6.9[a]	8, 7[b]	—	—	9[c]	—	169	37		63[d]	Oligo/meso.
Findlay	Pederson et al. (1976)	Net	—	10.3	—	—	—	—	25	59[e]		41[d]	Oligo/meso.
Chester Morse	Pederson et al. (1976)	Net	—	17.2	—	—	—	—	20	53[e]		47[d]	Oligo/meso.
Sammamish	Pederson et al. (1976)	Net	—	23.4	—	—	—	—	52	73[e]		28[d]	Meso.
Maggiore	Ravera (1969)	Net	7.5–8.9[f]	—	—	—	—	—	27	85		15[d]	Oligo.

[a] From Schindler (1972).
[b] Values are spring and summer TDP, respectively
[c] From one sample.
[d] Including *B. longirostris*.
[e] Not corrected for filtering efficiency.
[f] From Giussani et al. (1976).

TABLE 5. Percentage contribution of zooplankton species to average standing stocks (numbers unit volume^{-1} excluding nauplii) during the ice-free period for the nonacidic lakes. Species contributing <1% indicated by "+."

	Lake						
	Nelson 1976	Red Chalk	Blue Chalk	Harp	Jerry	Chub	Dickie
Copepoda							
Cyclopoid copepodid	12.8	29.0	11.1	21.4	28.5	32.7	9.0
Cyclops bicuspidatus thomasi	6.1	1.4	+	+	1.3	+	+
C. scutifer	2.8	2.8	1.4	+	+	1.5	+
Tropocyclops prasinus mexicanus	4.5	+	+	2.2	+	1.9	1.2
Mesocyclops edax	+	+	+	+	+	1.0	+
Cyclops vernalis	+			+	+		+
Eucyclops agilis							+
Paracyclops fimbriatus poppei			+				
Calanoid copepodid	25.1	33.0	52.3	39.8	47.3	37.9	33.1
Diaptomus minutus	19.2	15.9	20.8	8.4	14.8	16.5	24.5
D. oregonensis		2.1	+	+	+		+
Epischura lacustris		+	+	+	+	+	+
Senecella calanoides				+	+		
Diaptomus sicilis				+			
Cladocera							
Bosmina longirostris	27.4	2.7	2.4	12.1	1.1	+	+
Holopedium gibberum	+	+	+	10.4	+	3.3	15.0
Diaphanosoma leuchtenbergianum		2.7	+	3.4	2.9	1.4	1.8
Daphnia galeata mendotae		5.3	4.0	+	2.5	+	+
D. pulex		+	+		+	3.0	9.4
D. dubia	1.2	4.2			+		
D. retrocurva	+			+		+	+
D. longiremis	1.7	+				+	
D. ambigua		+	+			+	+
Eubosmina tubicen		+	+				3.6
Leptodora kindtii	+		+		+	+	+
Polyphemus pediculus		+			+	+	+
Sida crystallina		1.7	+				
Chydorus sphaericus	+			+			

species noted in the nonacidic lakes, the Clearwater Lake zooplankton community was characterized by the importance of *B. longirostris*, the absence of *Daphnia* sp. and the other common cladocerans *H. gibberum* and *D. leuchtenbergianum*, by the absence of the common copepods *T. prasinus mexicanus* and *Mesocyclops edax* and by the scarcity of *C. bicuspidatus thomasi* and *D. minutus* (Table 6).

The biomass averaged over the ice-free period of the zooplankton community of Clearwater Lake varied between 4.3 and 13.8 mg m^{-3}, and was significantly lower ($P < 0.01$, *t*-test of difference between means) than that of the nonacidic study lakes (Table 4). Cladocerans were much more important contributors to biomass than were copepods in the acidic lakes (Fig. 1). *Bosmina longirostris* comprised >95% of the cladoceran biomass in each year in Clearwater Lake (Table 4). *Cyclops vernalis* attained maximum densities in the early spring (Fig. 2). After it declined, *B. longirostris* formed virtually all of the community biomass (Fig. 1).

Average biomass for the ice-free period was not correlated with pH (or hydrogen ion activity) within the set of acidic lakes ($r = 0.04$, $P > 0.09$), nor for that matter within the set of nonacidic lakes ($r = 0.14$, $P > 0.06$). Zooplankton biomass was much lower in Hannah Lake, the lake with highest metal levels than in the other acidic lakes (Table 4). There was no correlation between Cu or Ni concentrations and zooplankton biomass when Hannah Lake data were excluded from the regression ($P > 0.7$). Excluding Hannah Lake data, zooplankton biomass in the acidic lakes was not correlated with pH ($r = 0.51$, $P > 0.1$). Although a rather large fraction of the variance in biomass could be attributed to phosphorus ($r = 0.62$, $P > 0.1$) or to total phytoplankton biomass ($r = 0.73$, $P > 0.05$), the coefficients of determination were not significant. With the exception of Lohi Lake, the reduction in biomass of the zooplankton communities in the acidic lakes was attributable to a reduction in the size of community dominants and to a reduction in densities. Lohi Lake had the highest zooplankton biomass among the acidic lakes but this level was exceeded by all of the nonacidic lakes. In contrast, the density of organisms in Lohi Lake (36.1 L^{-1}) exceeded the mean density of 33 individuals L^{-1} observed

TABLE 6. Clearwater Lake zooplankton species, 1973–78. Years and proportion of total collections (Rel. Freq.) in which species were observed are indicated. "+" indicates observation in only one sample.

Species	Years	Rel. Freq. %
Cyclops vernalis Fisher	1973–1978	81
C. bicuspidatus thomasi Forbes	1974, 1977	9
Diaptomus minutus Lilljeborg	1977, 1978	4
Epischura lacustris Forbes		+
Bosmina longirostris (O. F. Müller)	1973–1978	99
Chydorus sphaericus (O. F. Müller)	1973–1978	91
Ceriodaphnia megalops Sars	1973, 1974	28
Simocephalus serrulatus (Koch)	1975–1978	18
Polyphemus pediculus (L.)	1975–1978	7
Acantholeberis curvirostris (O. F. Müller)	1973, 1974	3
Eubosmina sp.		+
Macrothrix laticornis (Jurine)		+
Alona affinis (Leydig)		+

in the nonacidic lakes (Table 4). Given their apparent similarities in Cu, Ni, and TP concentrations and in pH it is not clear why the biomass is much higher in Lohi Lake than in Clearwater Lake.

Discussion

NONACIDIC LAKES

Copepodids were not identified to species in the study lakes. A comparison of the zooplankton communities

TABLE 7. Comparison of numerical composition of species (as percentages excluding nauplii) of the nonacidic study lakes with ELA lakes of similar morphometry and with nonacidic La Cloche Mountain lakes.

	Nonacidic lakes[a]	ELA lakes[b]	La Cloche Mountain lakes[c]
Number of lakes	7	37	19
Cyclopoid copepodid	20.6		
Cyclops bicuspidatus thomasi	1.3	17.5	19.3
Mesocyclops edax		9.4	7.9
Tropocyclops prasinus mexicanus	1.4	15.2	3.1
Cyclops vernalis		2.0	
C. scutifer	1.2		
Calanoid copepodid	38.3		
Diaptomus minutus	17.2	25.4	35.4
D. oregonensis		6.5	3.8
D. sicilis		2.1	
D. reighardi			1.2
Epischura lacustris		1.2	
Bosmina longirostris	6.5	6.1	13.1
Holopedium gibberum	4.1	4.3	3.4
Diaphanosoma leuchtenbergianum	1.7	2.3	5.7
Daphnia galeata mendotae	1.7	2.1	2.0
D. retrocurva		2.2	1.4
D. longiremis			1.4
D. catawba			1.2
D. pulex	1.8		
Other species	4.2	3.7	1.1

[a] Averages from Table 4.

[b] From Patalas (1971, Table 1) excluding community types I and IV.

[c] From Sprules (1975, Table 1) excluding lakes of pH < 5.0.

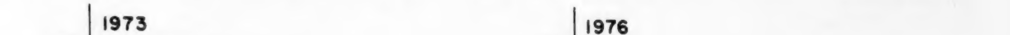

FIG. 1. Cumulative biomass of planktonic crustacea of Clearwater Lake, 1973–78.

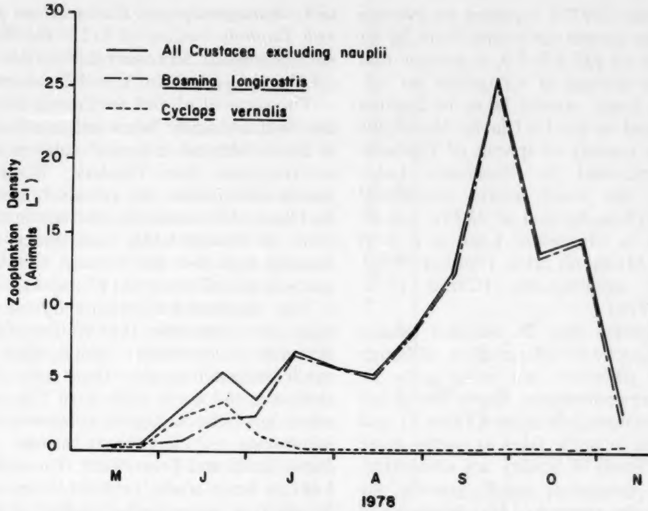

FIG. 2. Seasonal changes in the abundance of all crustacea (excluding nauplii), *B. longirostris* and *C. vernalis* in Clearwater Lake in 1978.

of the nonacidic study lakes with communities of nonacidic, morphometrically similar shield lakes in the La Cloche Mountains (Sprules 1975) and in northwestern Ontario (Patalas 1971) is complicated by the joint enumeration by Sprules of latter instar copepodids with adults (W. G. Sprules, Erindale College, Mississauga, Ont., personal communication) and by Patalas of all copepodids with adults (D. F. Malley, Freshwater Institute, Winnipeg, Man., personal communication). Nevertheless, there are many similarities. Seven species each formed >1% of the zooplankton densities in these three regions, namely *C. bicuspidatus thomasi*, *T. prasinus mexicans*, *D. minutus*, *B. longirostris*, *H. gibberum*, *D. leuchtenbergianum*, and *D. galeata mendotae*. These formed an average of 73 and 79% of the total densities in the ELA and La Cloche Mountain lakes, respectively (Table 7). Assuming that all calanoid copepodids were immature forms of *D. minutus*, these seven species formed between 72 and 93% of community densities in the nonacidic study lakes assuming, respectively, that none and all of the cyclopoid copepodids were either *C. bicuspidatus thomasi* or *T. prasinus mexicanus*.

There are, of course, differences in the communities between the regions attributable in part to differences in sampling regimens. Ten of the 28 species recorded by Sprules (1975) were not observed in the nonacidic study lakes. These occurred in a very small percentage of the lakes, however, and except for *Diaptomus reighardi*, they were never dominant. The general similarities of the communities in the three geographic regions is reasonable given the acceptance of at least the western half on the Canadian Shield as a single faunistic region with respect to planktonic crustacea (Patalas 1971). The communities of the acidic study lakes can therefore be assumed to have resembled those of the nonacidic study lakes at some time in the past prior to their contamination.

ACIDIC LAKES

In his survey of the zooplankton of ponds in Britain, Lowndes (1952) recorded 58 cladoceran species occurring over a pH range of 3.4–9.8, 23 of which occurred in ponds of pH <5.0. He recorded 59 copepod species occurring in ponds of pH 2.5–9.8, 26 of which occurred at pH <5.0. His reported ranges for *C. sphaericus* and *C. vernalis*, two commonly occurring species in Clearwater Lake, were 3.4–9.2 and 4.4–9.2, respectively. Given the evident capacity of so many zooplankton species to adapt to acidic environments, it is surprising that only 13 species of zooplankton were identified in Clearwater Lake (Table 6) in the six years of sampling. Roff and Kwiatkowski (1977) identified 11 and 13 species of crustacean zooplankton in two acidic lakes in the La Cloche Mountains in a much more restricted sampling program.

The zooplankton communities of Clearwater and the other acidic lakes clearly differed from the nonacidic lakes. Species richness was greatly reduced. Community biomasses were reduced because of the small size of the community dominant *B. longirostris*, and with the exception of Lohi Lake, because of reduced numerical densities (Table 4).

There were some similarities between the communities of the acidic study lakes and acidic La Cloche

Mountain Lakes. Sprules (1975) reported an average of 3.64 species in single sample collections from 28 La Cloche Mountain lakes of pH 3.8–5.0, a number that compares well with the average of 3.7 species per collection in Clearwater Lake. Acidic lakes in Sweden (Almer et al. 1978) and in the La Cloche Mountains are characterized by a scarcity of species of *Daphnia*. *Daphnia* was not recorded in Clearwater Lake. *Bosmina longirostris*, the most widely distributed cladoceran in Ontario (Brandlova et al. 1972), was an important zooplankter in Clearwater Lake as it is in the acidic La Cloche Mountain lakes (Sprules 1975) and in other acidic environments (Carter 1971; DeCosta and Janicki 1978).

Sprules (1975) reported that *D. minutus* usually dominated acidic La Cloche Mountain lakes, although *B. longirostris* or *H. gibberum* and occasionally *D. leuchtenbergianum* were codominant. These species are frequently important in nonacidic lakes (Table 7) and become more important in acidic lakes as species more sensitive to increased levels of acidity are eliminated. The importance of *C. sphaericus* and *C. vernalis*, the scarcity of *D. minutus*, the absence of *H. gibberum* and *D. leuchtenbergianum* and the dominance of the communities by *B. longirostris* make the communities of the acidic, metal-contaminated lakes described herein different from the communities of the acidic La Cloche Mountain lakes. As the acidic La Cloche Mountain lakes are similar to the acidic Sudbury area lakes in at least the phytoplankton component of their food base (Yan and Stokes 1978; Yan 1979) and generally similar in their location, morphometry, and trophic status, the difference in their communities is most likely attributable to the contamination of the Sudbury area acidic lakes with Cu and Ni.

Levels of Cu, Ni, Al, Mn, and Zn are elevated in the Sudbury study lakes reaching levels in Clearwater Lake of 97, 270, 450, 300, and 46 $\mu g\ L^{-1}$, respectively (Dillon et al. 1979). The toxicity of metals to zooplankton is related to oxygen and temperature regimes, to pH, and to the kinds and concentrations of inorganic and organic ligands. It is difficult to predict the toxicity of mixtures of metals as both additive and more than additive toxicities have been documented (Clarke 1974).

In Clearwater Lake, Dillon et al. (1979) reported that 55–95% of the copper existed as "free Cu" (determined by anodic stripping voltometry), the toxic metal species. Andrew et al. (1977) and Mierle and Stokes (1976) indicate that the toxicity of Cu may be somewhat reduced at the lake's low pH.

Biesinger and Christensen (1972) reported 16% reproductive impairment concentrations to *Daphnia magna* of 320, 30, and 22 $\mu g\ L^{-1}$ for Al, Ni, and Cu, respectively. Levels in Clearwater Lake approach these thresholds of toxicity for Al, and exceed them for Cu and Ni. Differences in tolerances among zooplankton species are to be anticipated. Baudouin and Scoppa (1974) report ratios of 48-h LC50s for *Cyclops abyssorum prealpinus*, *Eudiaptomus padanus padanus*, and *Daphnia hyalina* of 8:2:1 for Ni and of 70:10:1 for Cu with LC50 concentrations for *D. hyalina* being 1900 and 5 $\mu g\ L^{-1}$ for Ni and Cu, respectively.

The survival of and dominance by *B. longirostris* in the Sudbury acidic lakes indicate that this cladoceran is better adapted to heavy metal-contaminated, acidic environments than *Daphnia*, *H. gibberum*, or *D. leuchtenbergianum*, all of which occur in the acidic La Cloche Mountain lakes but not in the Sudbury acidic lakes. In Hannah Lake, metal concentrations were sufficiently high that the biomass of even *B. longirostris* was substantially reduced (Table 4).

The zooplankton community of Clearwater lake does not resemble the rotifer-dominated (usually *Brachionus urceolaris*) zooplankton communities of acidic, strip-mine ponds. These lakes tend to be smaller, shallower and more acidic than Clearwater Lake. They often have much higher concentrations of dissolved substances including heavy metals (Campbell et al. 1964; Smith and Frey 1971). The community of Cheat Lake, a large acidic (pH 4.5) impoundment in West Virginia, is quite similar to that of Clearwater Lake. DeCosta and Janicki (1978) observed that when crustacean biomass was at a maximum in Cheat Lake in the late summer, it was composed almost entirely of *B. longirostris*, as is that of Clearwater Lake. In Cheat and in Clearwater lakes, the maximum densities of *B. longirostris* were reached only after populations of the dominant invertebrate predator *M. edax* in Cheat Lake and *C. vernalis* in Clearwater Lake, had declined (Fig. 2). The Clearwater Lake data thus support the suggestion of DeCosta and Janicki that copepod predation may have a profound effect on instantaneous herbivore biomass in acidic as well as in nonacidic lakes (Kerfoot 1977). Unfortunately, metal data from Cheat Lake are not yet available (J. DeCosta, University of West Virginia, Morgantown, WV, personal communication).

PHYTOPLANKTON-ZOOPLANKTON INTERACTIONS

When Roff and Kwiatkowski (1977) attempted to determine the causal factors leading to reductions in diversity and abundance of zooplankton in acidic La Cloche Mountain lakes, they could not choose between direct toxic effects of depressed pH on zooplankton and indirect effects operating through changes in phytoplankton. The presence of Cu and Ni in the acidic Sudbury lakes described herein further complicates the determination of causes of changes in zooplankton communities. However, hypotheses can be constructed concerning how the acidification and heavy metal-contamination of Clearwater Lake affect the interaction of the zooplankton community with at least the phytoplankton component of its food supply. The ratinale for these hypotheses and their applicability to acidified lakes that do not have Cu and Ni problems are the subjects of the following discussion. The hypotheses are as follows:

1) Approximately 50% of the phytoplankton biomass of Clearwater Lake is unavailable as a food source to the zooplankton of the lake.

2) Changes in the structure of the phytoplankton community of Clearwater Lake are not attributable to zooplankton grazing.

3) The efficiency of energy transfer from phytoplankton to herbivorous zooplankton is reduced in Clearwater Lake as a result of its contamination.

The first hypothesis is consistent with the observation that the maximum size of particles ingested by filter-feeding Cladocera is correlated with the size of the zooplankter (Burns 1968). Using Burns' empirical relationship ($y = 22x + 4.87$) between the diameter (y in μm) of the largest bead ingested, and carapace length (x in mm) of a filter-feeding cladoceran, one would predict that the maximum size of particle ingested by a *B. longirostris* of carapace length 0.26 mm (the average carapace length of *B. longirostris* in Clearwater Lake) would be 10.6 μm. Gliwicz (1969) found that although particles up to 14 μm in diameter were occasionally ingested, 85% of particles ingested by *B. longirostris* and *coregoni* were <5 μm in diameter.

From 1973 to 1978, dinoflagellates formed an average of 45% of the ice-free period phytoplankton biomass in Clearwater Lake (Yan 1979). Most (generally over 85%) of this was attributable to *Peridinium inconspicuum*. The average diameter of *P. inconspicuum* was 14 μm (mean length of axes of 300 measured individuals). On 2 days (one in 1976 and one in 1977) on which *P. inconspicuum* formed almost all of the phytoplankton biomass, the guts of 10 large ($\simeq$0.4 mm carapace length) *B. longirostris* were removed and the contents examined under compound microscopes. No *P. inconspicuum* were observed although identifiable algae were present in the gut contents indicating that *P. inconspicuum*, although it is small for a *Peridinium*, is rarely ingested by *B. longirostris*. The dominant phytoplankter, comprising almost half of the phytoplankton biomass is most probably unavailable as an energy source to the dominant zooplankter of Clearwater Lake.

As a great many algal species tolerate the acidic, metal-contaminated conditions of Clearwater Lake (Yan 1979), it is attractive to suggest that the domination of the phytoplankton community of the lake by *P. inconspicuum* is not attributable to its greater tolerance of the lake's contaminated conditions, but to the selective removal by filter-feeding zooplankton of smaller (i.e. more edible) taxa. Of the 55% of the average phytoplankton biomass in Clearwater Lake not attributable to dinoflagellates, 80% on average was attributable to four taxa — *Oocystis* sp. (cells 5 μm in diameter, 8 μm in length), *Chlamydomonas* sp. (cells 3 μm in diameter, 6.5 μm in length), an unidentified chrysomonad (cells 3 μm in diameter, 2.5 μm in length and *Cryptomonas* sp. (cells 11 μm in diameter, 14 μm in length). Except for *Cryptomonas*, these genera are of a size that could readily be ingested by *B. longirostris*, although all phytoplankton that are ingested are certainly not assimilated (Porter 1975). *Oocystis* was identified in the contents of the guts of the *B. longirostris* that were examined.

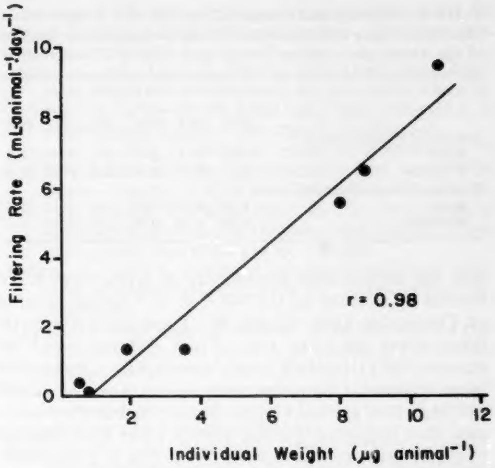

FIG. 3. Relationship between dry weight of filter feeding zooplankton and filtering rates. Filtering rates for *Diaphanosoma* sp., *Bosmina longirostris*, *Diaptomus oregonensis*, *Chydorus sphaericus*, *Daphnia rosea*, *D. galeata mendotae*, and *Holopedium gibberum* are from Haney (1973). Weights are from Table 2 or are available from the authors on request.

The effect that filter-feeding zooplankton exert on phytoplankton community structure increases with increases in the ratio of herbivorous community filtering rates to phytoplankton renewal rates. The most important determinants of community filtering rates are the size of the individual zooplankters which determines their filtering rate (Fig. 3) and their densities, the product of which is the community biomass. As the zooplankton biomass in Clearwater Lake was substantially reduced in comparison with the nonacidic study lakes, while phytoplankton biomass (Yan 1979) and renewal rates (Dillon et al. 1979) were not reduced, the capacity of the zooplankton to effect changes in the phytoplankton community via their grazing activities is reduced in Clearwater Lake in comparison with the nonacidic lakes.

The extent of this reduction can be estimated assuming filtering rates calculated for *B. longirostris* will approximate community filtering rates in Clearwater Lake (Fig. 2). Haney (1973) measured a filtering rate of 0.44 $\text{mL} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ for *B. longirostris*. Using this measured rate and the numerical densities of *B. longirostris* in Clearwater Lake rates, it was calculated

TABLE 8. Average and maximum density of *B. longirostris* in Clearwater Lake and calculated average and maximum fraction of the whole lake volume filtered each day by *B. longirostris*.

	Year					
	1973	1974	1975	1976	1977	1978
Number of *B. longirostris* L^{-1}						
Mean	6.0	6.7	5.1	9.1	17.2	6.9
Maximum	20.6	62.4	21.9	28.2	54.1	25.6
% of whole lake volume filtered day^{-1}						
Mean	0.26	0.73	0.22	0.40	0.75	0.31
Maximum	0.90	2.86	0.97	1.23	2.42	1.12

that the zooplankton community of Clearwater Lake filtered an average of 0.22–0.75% d^{-1} of the volume of Clearwater Lake (Table 8). These rates are 5–18 times lower than the rate of 4% d^{-1} measured by Haney (1973) in Halls Lake, a nonacidic oligotrophic lake in Ontario near the study lakes. The calculated filtering rates are only approximations, but they indicate that herbivore grazing should exert little control over phytoplankton community structure in Clearwater Lake. The importance of dinoflagellates in Clearwater Lake and most likely in the acidic La Cloche Mountain lakes that are not contaminated with Cu and Ni is therefore likely not a consequence of the selective removal of smaller taxa by herbivores. It is probably a manifestation of differences in tolerance among algal species to rapid decreases in (Yan and Stokes 1978) or to low pH.

Smith and Frey (1971) suggested from their studies of strip-mine ponds in Indiana that the efficiency of energy transfer from phytoplankton to zooplankton was reduced in their acidic ponds. The low filtering rates calculated for Clearwater Lake support this suggestion. Data from acidic lakes that do not have associated Cu and Ni problems are scanty, but suggest that standing stocks are low (Roff and Kwiatkowski 1977) and smaller grazers (*B. longirostris* or *D. minutus*) replace larger grazers (*Daphnia*). We can thus hypothesize that the efficiency of energy transfer from primary to secondary trophic levels will be reduced by acidification.

These hypotheses that the efficiency of energy transfer from primary to secondary trophic levels is reduced by acidification, and that changes in phytoplanton community structure that occur as lakes acidify are not related to grazing, are presented to provide directions for research. The data from which the hypotheses were derived are from Sudbury lakes that have been acidic and contaminated with Cu and Ni for many years. Hypotheses constructed to explain relationships in these lakes should be tested in lakes that have been recently acidified, have no associated Cu or Ni problems, or are at sufficiently early stages of acidification that lake pHs fluctuate markedly with time.

The testing of hypotheses similar to those presented in this report necessitates the collection of quantitative measures of seasonal and annual variations in the structure of entire zooplankton communities (Protozoa, Rotifera, Crustacea, and Insecta). It also requires estimates of production at the level of the entire communities and of community interactions. These are laborious tasks, but with recent indications (Dillon et al. 1978) that a great number of Precambrian Shield lakes in Ontario may soon acidify, the need to understand changes in the dynamics of biotic communities in acid lakes is of paramount importance.

Acknowledgments

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Differential Prey Vulnerability and Predator Selectivity: Effects of Evasive Prey on Bluegill (*Lepomis macrochirus*) and Pumpkinseed (*L. gibbosus*) Predation

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VINYARD, G. L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) predation. Can. J. Fish. Aquat. Sci. 37: 2294–2299.

Sunfish will select *Daphnia* preferentially over copepods even though the apparent size of the copepods may be considerably larger. This selectivity is probably the result of the fishes having learned differences in the evasion capabilities of the two different prey types, and having translated this into a differential selectivity. Sunfish have the ability to correlate information about the evasion capabilities of prey with visual appearances of the prey, and to select less evasive prey. Such information may have considerable significance in defining the observed selectivity of these fish in nature, and such behavioral responses should be considered in future modeling efforts.

Key words: predation, *Lepomis*, selectivity, behavior

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Les crapets choisiront *Daphnia* de préférence aux copépodes, même si la taille apparente de ces derniers est beaucoup plus grande. Cette sélectivité résulte probablement du fait que les poissons ont appris les différences d'aptitude à l'évasion des deux types de proies et ont traduit cette connaissance en une sélectivité différentielle. Les crapets sont capable d'établir la relation entre l'information concernant la capacité d'évasion des proies et l'apparence visuelle de ces dernières et de choisir la proie moins évasive. Une telle information peut être très importante quand il s'agit de définir la sélectivité observée chez ces poissons dans la nature, et les réponses éthologiques de ce genre devraient être considérées dans les modélisations futures.

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THE analysis of planktivorous fish predation in natural situations usually yields a pattern of selective prey consumption in which certain members of the potential prey array are more heavily consumed than others. It has been widely confirmed that prey size is usually a dominant factor influencing the selectivity of visual planktivores, with such size-selective predation generally falling most heavily on the largest zooplankters present (Brooks and Dodson 1965; Gailbraith 1967; Hrbacek et al. 1961; Wong and Ward 1972). There are, however, examples of planktivory in fish not readily explained on the basis of size relationships alone, and even within the observations of size-related predation there are occasionally unexplained deviations from the accepted paradigm (Brooks 1968; Ivlev 1961; Zaret 1980). Recently, it has also been demonstrated that the criterion of prey selectivity for nonvisual planktivores can shift from size to current sensing and evasion capabilities (Drenner 1977; Drenner et al. 1978). In what follows, I will describe how a consideration of certain behavioral mechanisms may enlarge our understanding of selective predation in visual fish planktivores. These behavioral components include factors such as preference of the fish and prey evasion which, when coupled with the predator's experience, can alter the observed prey choice by expanding the criteria upon which the fish select prey. The evasion capabilities of zooplankton prey and the effects of learning on prey selection have not previously been investigated to determine if planktivorous fish can retain and utilize information about prior contacts with different kinds of prey.

The occurrence of selection mechanisms including elements distinct from simple prey-size relationships has not often been considered by modelers of planktivore predation. Most recent models of planktivore prey selection (Werner and Hall 1974; O'Brien et al. 1976; Eggers 1977) have used the prey size frequency distribution as the primary input defining selectivity of planktivorous sunfish. The model of Confer and Blades (1975) is exceptional in that it did consider differential rates of capture success between zooplankton types and some of the potential effects of motion on reactive distance.

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To predict the prey captured, the prey selection models of Werner and Hall (1974) Confer and Blades (1975), and of Eggers (1977) all require low prey densities and nonsimultaneous encounters at the reactive distance, while the apparent size model of O'Brien et al. (1976) accommodates higher prey densities and the potential for multiple prey encounters. Since the apparent size model is sufficiently robust to produce acceptable predictions of prey eaten by planktivorous sunfish in situations where the prey array consists of a single species divided into several size-groups (O'Brien et al. 1976; Wright et al. 1980), I will consider some of the assumptions and requirements of this model with two alternate prey types to establish if the model may be directly useful in multispecies situations.

Apparent Size

The apparent size model (O'Brien et al. 1976) invokes one of two mechanisms for prey selection depending upon the density of the prey and their respective reactive distances. When prey density and/or visibility is low, single prey are encountered at the predator's reactive distance for them and fish are assumed to eat prey as encountered. This is identical to the results predicted by the models of Werner and Hall (1974) and Confer and Blades (1975). However, when visibility and/or prey density are high, the apparent size model predicts that the fish choose between simultaneously encountered prey on the basis of the apparent size of the prey. Apparent size can be computed as the maximum visual angle subtended by prey (O'Brien et al. 1976). Thus a small prey might have a larger apparent size than an actually larger but more distant prey.

Evasion

Brooks (1968) reported the results of an experimental feeding trial in which alewives (*Alosa*) were allowed to feed on concentrated plankton sample consisting primarily of several instars of *Diaptomus minutus* and significant numbers of *Daphnia catawba*. He found that the Daphnia were very quickly consumed, and that removal of *Diaptomus* followed in order of diminishing instar size. Such a sequential consumption of the *Diaptomus* beginning with the larger individuals is predicted at high prey densities by most planktivore models; however, the immediate elimination of *Daphnia* is not adequately predicted by any of the current models. Although Brooks does not report the actual sizes, probable size differences between the *Daphnia* (1–1.5 cm, Brooks 1959) and the *Diaptomus* (1 mm, Wilson 1959) should not have been sufficient to account for the immediate and virtually complete removal of the *Daphnia*, and thus the mechanism of their elimination remains unexplained.

Others have observed that certain Cladocera may be relatively abundant in the diet of many planktivorous fish, whereas copepods of approximately equal size tend to be relatively underrepresented in the diet (Allan 1976; Zaret 1980). Such findings run counter to arguments of a purely size-related predation by fish.

Two alternate, though not exclusive, processes which might account for the immediate disappearance of the *Daphnia* can be proposed. There might be a significant preference by the fish for *Daphnia* which could direct their predation toward them. Alternatively, the *Diaptomus* might have possessed greater abilities for evasion than the *Daphnia*, and thus not been as vulnerable to the fish. Such enhanced evasion by *Diaptomus* would be effective independent of the capture method being employed by the alewife (Janssen 1976, 1978).

Choice Modification

The data suggest that if the fish can identify differences between potential prey, then they may be able to utilize such information to modify their selectivity. Can sunfish concentrate their predation on particular prey types which are determined by experience to be more easily captured or do they have more permanent preferences which are maintained in a variety of situations?

Procedures

To test the effects of different prey types on the apparent size choice relationship, I performed a series of 185 feeding trials, using a long plexiglass aquarium (1 m × 20 cm × 20 cm) in which bluegill (*Lepomis macrochirus*) were conditioned to swim through a short z-maze at one end of the tank to receive food. The z-maze prevented the fish from seeing into the prey presentation area of the tank until it had rounded the last corner, and thus provided a virtually simultaneous encounter with both prey types. The fish were then presented with choices between a cladoceran, *Daphnia pulex*, and a copepod, *Diaptomus pallidus*, both of which had previously been measured (top of head to base of tail spine or total body less caudal setae) with an ocular micrometer under a dissecting microscope. Sizes ranged from 0.66 to 1.33 mm. Fish were familiar with both prey types. Conditioning fish to maze swimming was accomplished over several days with commercial flake fish food.

As the fish selected prey, the first pursued was scored as the choice. Both prey were encountered within the reactive distance of the fish as it left the maze. In such experiments, the position of both prey and the fish were noted relative to a meter scale at the bottom of the aquarium when the fish began pursuit. This usually was soon after the fish passed through the last opening of the maze.

Upon completion of feeding, conditioned fish normally returned through the maze without coaxing, ready for the next trial. Zooplankton prey in these trials were not restrained and constant monitoring of their position was required. Trials in which their position changed drastically up or down from midwater or along the axis of the aquarium were omitted.

To examine the potential of *Diaptomus* for evasion, I allowed small bluegill sunfish to feed on prey populations of forty 1 mm *Diaptomus pallidus* in 2-L crystalizing bowls. The fish were starved for 24 h prior to trials but had regularly been fed both *Diaptomus* and *Daphnia* previously. Fish were observed while they made 20 active attempts to capture prey (involving an actual "snap" of the mouth directed at the prey) after which the fish were removed and immediately examined to determine the actual numbers of prey ingested.

The experimental procedure adopted to test the abilities of sunfish to alter their selectivity was intended to mimic the natural situation of sunfish encountering two visually distinct prey types which also differ in their relative evasion capabilities. This is an appropriate model for fish confronting both cladoceran and copepod prey in nature.

The experiments involved training eight (avg. TL = 34 mm, SD = 2.4) pumpkinseed sunfish (*Lepomis gibbosus*) to swim through a simple z-maze at the end of which they were confronted with a choice between two visually distinct prey types, one which randomly evaded capture 50% of the time and the other which never evaded capture. The prey choice consisted of two *Daphnia pulex*, one stained with neutral red, the other with alcian blue. In one series of experiments, the *Daphnia* were both the same size, while in a later series with the same fish they were of different known sizes. The evasion or capture was affected by placing each pray in a glass tube connected by rubber tubing to a syringe. Capture was permitted by flushing a prey from its tube, evasion by drawing both *Daphnia* back up the tubes out of visual contact with the fish. A choice was defined as a capture attempt involving actual contact of the fish with the tube containing the selected prey. To overcome any intrinsic color bias, half the fish were trained with red prey evading, half with blue. Decisions concerning right or left tube position for red or blue presentation and whether or not to deliver the evading prey were made randomly before the initiation of a trial series. Fish were conditioned to maze running using amphipods and commercial flake food. During experimentation they were maintained on these foods and received *Daphnia* only from tubes during trials. Trials were run under ambient room illumination supplemented with a 20-W fluorescent tube placed 30 cm above the tank.

During the trials, there was often a period of a few seconds during which the fish would sit nearly motionless in position a few centimetres from both tubes looking alternately back and forth at the tubes prior to actual choice. There were normally 20–25 trials per day for each fish.

Results

Fish tended to select *Daphnia* even when the apparent size of a simultaneously encountered *Diaptomus* was larger (Fig. 1). This suggests a substantial preference for the *Daphnia* in multiple encounter situations.

Selection for Daphnia in the apparent size choices might be explainable if there was a higher detection probability for the *Daphnia*. This seems unlikely given the similarity of the reactive distances for various copepods and *Daphnia* (Confer and Blades 1975). In addition, independent reactive distance measurements for *Daphnia* reported by Werner and Hall (1974) and Vinyard and O'Brien (1976) are also similar to the reported copepod reactive distances. Differential detectability seems not to provide an explanation for the observed selection for *Daphnia*.

Of 33 fish (avg. total length = 49 mm, SD = 6.9 mm) consuming copepods, the capture success averaged 49.9% (SE = 3.90). Capture success for sunfish consuming *Daphnia* is virtually 100% and successful evasions by *Daphnia* are exceedingly rare. Evidently both preference for *Daphnia* and evasion by *Diaptomus* may contribute to restricting the feeding of sunfish to *Daphnia* when the plankters cooccur.

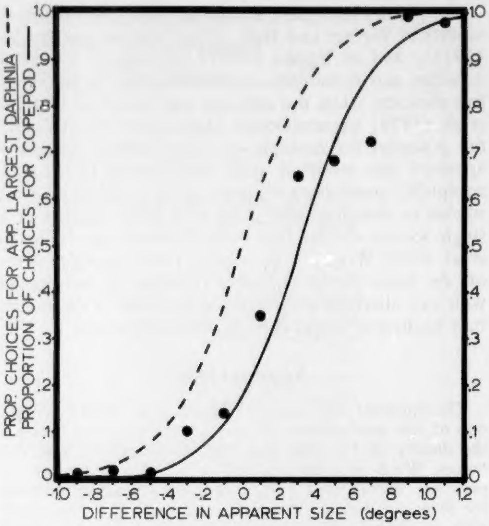

FIG. 1. Plot of apparent size choice experiments in which sunfish were presented with a choice between a *Diaptomus pallidus* and a *Daphnia pulex*, or between two *Daphnia*. The dashed line representing the choices between two *Daphnia* is a fitted hyperbolic tangent function from O'Brien et al. (1976). The proportion of choices for the copepod (*Diaptomus*) is plotted versus difference in apparent size of the two prey (*Diaptomus* minus *Daphnia*) when the fish initiates pursuit. Points on the graph represent average values obtained for apparent size difference intervals of 0.1° with a total of 185 observations. The solid line is a least-squares fitted hyperbolic tangent function, $Y = \tanh (X - 0.306)/2.5$ which is a better fit than a simple linear regression line.

Another observation which suggests that sunfish recognize copepod and cladoceran prey is that their capture techniques for the two prey types are substantially different. Fish familiar with both prey types utilize an active and vigorous capture motion when capturing copepods, while the capture of *Daphnia* is accomplished in a comparatively leisurely fashion. Janssen (1978) reported similar behavior for the alewife. Such differences indicate that the fish are discriminating between prey types, and that they modify capture techniques to maximize probability of capture of more active prey.

In the choice modification experiments the fish showed a definite tendency to select prey which did not evade (Fig. 2). In general, as the total number of trials increased, the average percentage of choices for the nonevading prey reached a maximum value of about 90–95%. The fish learned to associate a visual aspect of the prey with its subsequent behavior, and then modified their selectivity to maximize captures.

In the experiments in which there were different

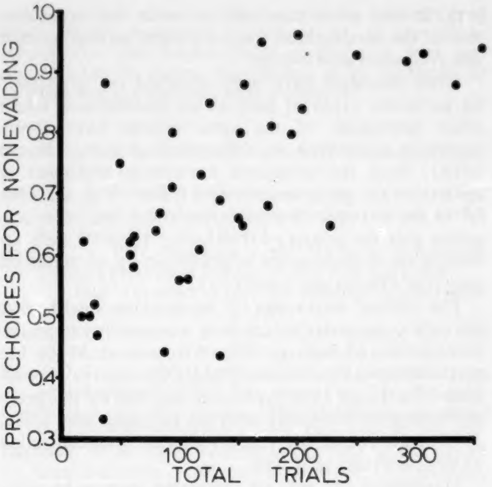

FIG. 2. Plot of the proportion of choices by sunfish for the nonevading prey versus the total number of trials with both prey types. The evading prey had an a priori determined probability of evasion of 50%. Points represent averages from each daily experimental session with each fish. There were 20–25 trials per fish per day.

sizes of *Daphnia* prey, the fish tended to select the larger, evasive prey as their size increased relative to the nonevasive prey. As the ratio of the size of the evasive to nonevasive prey increased, the fish increasingly selected the evasive prey even though the capture rate remained 50% (Table 1).

These experiments are particularly relevant to considerations of optimal foraging in fish (Eggers 1977). Optimal foraging theory (Schoener 1971) predicts that the predator should select from the prey array that subset which yields the greatest net rate of return of biomass. In terms of the current experimental design, optimally foraging fish should restrict predation to the nonevasive prey until the size of the 50% evasive prey is more than twice that of the nonevasive prey. They should then shift over to preying completely on the evasive prey for which the net return per prey encountered will be greater despite the 50% capture rate. This type of tactic can be contrasted with simpler selection processes in which the fish either continues to select nonevasive prey in spite of their smaller relative size, or in which the fish simply selects the larger prey regardless of evasion. The latter selection pattern might be considered typical of prey-size maximizers, while the former might be typical of capture-frequency maximizers. The results of the experiments (Table 1) are not entirely consistent with any of these tactics and suggest that although the fish tend to operate as optimal foragers there is also some tendency to operate as prey-size maximizers.

TABLE 1. Observed choices made by fish between different sizes of evasive and nonevasive prey and predictions based on different assumed foraging strategies. Values given in the table are percentages derived from over 2800 choices made by the sunfish between pairs of stained evasive and nonevasive *Daphnia* of known sizes. Evasive prey were successfully captured in 50% of their encounters. Biomass was computed from length using the relationship found in Edmondson and Winberg (1971).

	Biomass ratio (evading/nonevading)		
	<1.0	1.0 to 2.0	>2.0
Observed frequency of choosing evasive prey	0.20	0.44	0.73
Expected frequency of choosing evasive prey if predator is operating as an optimal forager[a]	0	0	1.0
Expected frequency of choosing evasive prey if predator is operating as a prey-size maximizer[a]	0	1.0	1.0
Expected frequency of choosing evasive prey if predator is operating as a capture-frequency maximizer[a]	0	0	0

[a] Predators are assumed to make no mistakes in choosing prey in accordance with their foraging strategy.

Discussion

The data strongly indicate that sunfish can use information concerning the size and evasion capabliity of visually distinct prey types to modify both their prey selectivity and capture behavior for increased return. This suggests a substantial level of plasticity in sunfish prey selection which has not previously been identified. That the fish can, and regularly do, use these behaviors in the field is not yet demonstrated, but the potential for (and high probability of) such activities and the potential ecological impact of this behavior should not be ignored.

Ivlev (1961) recognized that the selectivity of predatory fish might be changed by experience with different food types and by the relative abilities of different prey to evade or discourage predators. He found that conditioning carp to a particular prey increased their selection for that prey in subsequent tests involving alternate prey. When fish predators were exposed to prey with different maximum swimming speeds (all of which could be captured), they preferentially ate the most sluggish. He thus demonstrated that selectivity of fish for various prey could be altered by both the experience of the fish (training bias) and by the evasion capabilities of the prey.

The tendency for predators to concentrate their predation on a certain subset of the potential prey array has variously been attributed to the formation of search images (Tinbergen 1960; Mook et al. 1960) or to a tendency for the predator to limit search to more profitable patches (Royama 1970a, b; Gibb 1958, 1962). In both cases the predator must assess the relative rate of return involved in hunting either for a specific type of food or in deciding which patches have the highest rate of return. Thus, some mechanism analogous to that shown by the sunfish is required to bring about the discrimination necessary for such behaviors.

The findings reported here for sunfish are similar to those reported for great tits (Gibb 1958, 1962; Smith and Dawkins 1971) in that fish concentrate their predation on food types yielding the highest rate of capture. In addition, the experiments show that sunfish are capable of assessing an expectation of return which is correlated with specific visual characteristics of the prey organisms rather than with a location-associated search.

Ivlev (1961) examined the unconditioned electivities of planktivore bleak (*Alburnus alburnus*) for several common zooplankton species. While electivity values for *Daphnia* were always highest among tested prey, electivities for *Bosmina* were consistently higher than for *Diaptomus*. Actual length measurements, or species identities for the zooplankton used were not reported, but in general *Bosmina* tend to be quite small and *Diaptomus* larger as adults. Thus the observed prey selection of the planktivore bleak used by Ivlev are not in accord with an entirely size-defined selection process.

Sunfish exhibit prey selection behavior in which the criteria of choice include the probability of capture of the prey as well as its size. Risk of capture for prey of fishes has generally been thought to follow a positive linear relationship of greater risk with increasing size of the prey (Ware 1973; Werner and Hall 1974; Confer and Blades 1975; Vinyard and O'Brien 1975). Modification of prey risk by experience of the fish might have considerable impact on predation rates observed on different zooplankton groups in the field. For example, for fish experienced with copepods and also often exposed to *Daphnia* there may be a relatively greater motivational threshold to be overcome before the fish will pursue the copepod. Thus risk for evasive copepods might be effectively reduced by cooccurrence of an equivalent sized (or even smaller) *Daphnia*. Conversely, risk to *Daphnia* might be substantially increased by the predator's familiarity with evasive copepods. Thus, at moderate or high prey densities in diverse zooplankton communities prediction of relative rates of predation based solely on differences in reactive distance between different prey groups might contain considerable error, due to differences in likelihood of pursuit and capture. Precision in models such as that of Confer and Blades (1975) which included both copepod and cladoceran prey might be enhanced by relating prey risk to factors such as the probabilities of coincident occurrence and capture of the various prey. It may prove necessary to assess risk as a function of the zooplankton species present as well as their size-frequency distribution.

Some predators have been observed to "specialize" on particular types of prey in an environment where other individuals of the same species have simultaneously specialized on different food types (Bisson 1978). Such specializations have been attributed to tendencies for predators to select foods which are similar to the last type of prey eaten, and it has been suggested that the primary evolutionary value of such actions is the concentration of predation on an abundant prey type (Bryan and Larkin 1972).

The vertical migrations of zooplankton might serve not only to generally reduce their vulnerability to predation (Zaret and Suffern 1976; Wright et al. 1980) but may also serve to continually shift the relative proportions of different prey types and thus reduce the predator's level of familiarity with the potential prey array. This could retard the rate of predator specialization on any particular prey type.

Maximizing the rate of successful capture by preferentially selecting nonevading prey is generally in accordance with optimal foraging theories (Schoener 1971; Eggers 1977). When evasive prey are smaller than the nonevasive prey there should be much more predation on the nonevasive prey. When the evasive prey are larger but not so large that their size compensates for the reduced capture rate, the optimally foraging predator should still select the nonevasive prey to maximize its rate of return per encounter (Table 1). However, as the size of the evasive prey increases to outweigh the lower capture rate, an optimal forager should shift to the larger evasive prey for which the average net return per encounter would be greater. Predators operating as size-maximizers ought to select larger prey regardless of rate of capture. Capture-frequency maximizers ought to continue to select nonevasive prey regardless of size. The actual observations (Table 1) indicate that the fish are not capture-frequency maximizers. It is however impossible from the data to eliminate either the optimal forager or size-maximizer strategies.

In conclusion it is apparent that sunfish have substantial abilities to adjust their prey selectivity to the particular prey array present. This ability is likely evolutionarily significant in allowing the fish to exploit the locally most vulnerable prey and thus be more closely attuned to the conditions of their environment. This ability would also allow predators to exploit temporally changing prey with different vulnerabilities and may provide the basis for predators to operate as optimal foragers.

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Depression of Primary Productivity by Humic Matter in Lake and Reservoir Waters of the Boreal Forest Zone

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Analysis of water from backwater and main-stem regions of three reservoirs and a natural lake belonging to major river systems in northern Manitoba (Canada) showed that primary productivity was inversely related to total "dissolved" (<0.45 μm) organic carbon and nondialyzable dissolved iron, organic carbon, nitrogen, and H-bonded polymeric hydroxyl groups. The chemical data apparently represent allochthonous humic–FeOOH complexes with strong, covalent metal-ligand bonds. The results suggest that humic matter depressed primary productivity by making iron unavailable to phytoplankton, but not by attenuating light, lowering the pH, or sequestering phosphate (although the dissolved phosphorus appeared to be mostly in the form of humic-iron-phosphate complexes). Relatively stagnant backwater bays, where humic mater accumulates, were less productive than the more rapidly flushed, less humic main-stem waters. In addition, the reservoirs, which had been formed 6 mo, 3 yr, and 14 yr prior to the time of sampling, revealed short-term anomalies caused by impoundment. Evidently three distinct stages of geochemical and trophic development are represented, the sequence of stages being tentatively generalized as follows for reservoirs of this region: (1) soon after impoundment, rapid leaching of nutrients from submerged land causes a brief rise in productivity and aberrantly high levels of dissolved low molecular weight phosphorus and nitrogen in the backwaters; (2) subsequently, a "pulse" of soil humic matter released more gradually into the backwaters depresses productivity by fixation of minor elements such as iron, even if the dissolved phosphorus levels are high; (3) finally, a steady state is restored when this anomalous accumulation of humic matter is removed from the water column by sedimentation or flushing, allowing productivity to return to higher levels. But even under unperturbed natural conditions humic matter restricts the productivity of surface waters in this geographic region to a greater or lesser extent.

Key words: humic matter, organic matter, primary productivity, iron, lakes, reservoirs, nutrient availability, Canadian Shield, water quality, phytoplankton ecology

JACKSON, T. A., AND R. E. HECKY. 1980. Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone. Can. J. Fish. Aquat. Sci. 37: 2300–2317.

L'analyse de l'eau des régions de renvoi et de l'axe hydrographique de trois réservoirs et d'un lac naturel faisant partie de réseaux fluviaux majeurs du Manitoba septentrional (Canada) démontre que la productivité primaire est en relation inverse avec le carbone organique « disssous » (<0,45 μm) total, le fer, le carbone organique et l'azote dissous non dialysables, et avec les groupes hydroxyl polymériques à liaison hydrogène. Les données chimiques représentent apparemment des complexes humiques–FeOOH allochthones avec fortes liaisons covalentes fixatrices de métaux. Les résultats suggèrent que la matière humique abaisse la productivité primaire en rendant le fer hors de portée du phytoplancton, sans toutefois atténuer la lumière, abaisser le pH ou séquestrer les phosphates (bien que le phosphore dissous semble en grande partie sous forme de complexes humiques-fer-phosphates). Les baies relativement stagnantes de la région de renvoi, où s'accumule la matière humique, sont moins productrices que les eaux de l'axe principal, à vidange plus rapide et moins humiques. De plus, les réservoirs qui avaient été formés 6 mo, 3 ans et 14 ans avant l'échantillonnage montrent des anomalies à court terme causées par la retenue des eaux. Trois stades distincts de développement géochimique et trophique sont bien représentés, l'ordre de ces stades étant provisoirement généralisé comme suit pour les réservoirs de cette region : (1) peu après la retenue, le ruissellement rapide des nutriments du sol submergé entraîne une brève élévation de productivité et des niveaux anormalement élevés de phosphore et d'azote de faible poids moléculaire disssous dans les eaux de renvoi; (2) ensuite, une « pulsation » de matière humique du sol mise en liberté plus graduellement dans les eaux de renvoi abaisse la productivité par fixation d'éléments mineurs,

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tels que le fer, même si les niveaux de phosphore dissous sont élevés; (3) finalement, l'équilibre se rétablit quand cette accumulation anormale de matière humique est enlevée de la colonne d'eau par sédimentation ou vidange, permettant à la productivité de retourner à des niveaux plus élevés. Mais, même dans des conditions naturelles non perturbées, la matière humique limite la productivité des eaux de surface dans cette région géographique à un degré plus ou moins grand.

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CREATION of reservoirs by impoundment of river water causes marked changes in the physicochemical properties, trophic status, and biota of the water (Zhadin and Gerd 1961; Rzoska 1966; Campbell et al. 1975). There is usually an initial upsurge of biological production followed by a decline a few years later; finally, after several years, productivity may return to higher levels as long-term steady-state conditions are reestablished (Lapitsky 1968; Lowe-McConnell 1973). The initial increase in production is probably caused by release of soluble nutrients from inundated soil and vegetation (Zhadin and Gerd 1961; Lowe-McConnell 1973; Campbell et al. 1975; Ostrofsky and Duthie 1978). The subsequent "trophic depression phase" is not well understood, but possible reasons for it include (1) exhaustion of readily available nutrients, (2) fixation of nutrients in unavailable forms by humic matter and other binding agents leached or eroded into the water from submerged soil or peat, (3) attenuation of light by dispersed humic matter or soil particles, (4) lowering of the ambient pH by humic matter, and (5) release of toxic organics such as phenols into the water (Baranov 1961; Duthie and Ostrofsky 1974; Hecky and Harper 1974). Although allochthonous humic matter derived from soil occurs widely in unperturbed natural waters (Bordovskiy 1965) as well as reservoirs (Gjessing and Samdal 1968; Campbell et al. 1975) and is relatively abundant in cool, moist regions, flooding could increase the concentration, or alter the inherent character, of the humic component of the water.

Humic matter may play an important role in aquatic ecology, largely by affecting the bioavailability of nutrients and toxic substances. Although humic matter can promote the growth of algae, bacteria, and plants (Burk et al. 1932; D'yakonova 1962; Prakash and Rashid 1968; Nechutová and Tichý 1970; Vaughan 1974; Milanovich et al. 1975; de Haan 1976; Giesy 1976), it may also inhibit biological activity by fixation of trace metals or phosphate (Sakamoto 1971; Golterman 1973; Goodman and Cheshire 1973), by inhibition of enzymes (Butler and Ladd 1971), or by absorption of light or lowering of the ambient pH (Shapiro 1957). Humic complexes of iron and aluminum readily bind phosphates (Weir and Soper 1963; Lévesque and Schnitzer 1967; Lévesque 1969; Sinha 1971; Jackson and Schindler 1975). The ecological significance of this phenomenon is unknown, but the importance of phosphorus as a limiting nutrient in many inland waters (Vollenweider 1968; Schindler 1974, 1977) and the abundance and widespread occurrence of humic matter in natural waters and sediments (Bordovskiy 1965) suggest that the binding of phosphorus by humic matter could have an effect on primary production in lakes and reservoirs (Golterman 1973).

This report presents the results of a comparative study of humic matter, nutrients, and primary production in three reservoirs and one natural lake located in a cool, moist, forested region where humic matter is abundant. These bodies of water are situated in essentially the same geographic and environmental setting, but the reservoirs differ in the time elapsed since the water level was raised. Our purpose was (1) to test the hypothesis that fixation of phosphorus or other nutrients by dissolved or dispersed humic substances may limit primary productivity in lakes and reservoirs, and (2) to study anomalous effects due to impoundment.

Field Area, Materials, and Methods

SAMPLING LOCALITIES

The bodies of water investigated were the Notigi, Kettle, and Kelsey reservoirs, and Southern Indian Lake (together with two streams flowing into the lake) in northern Manitoba, Canada (Fig. 1; Table 1). The Rat River flows into

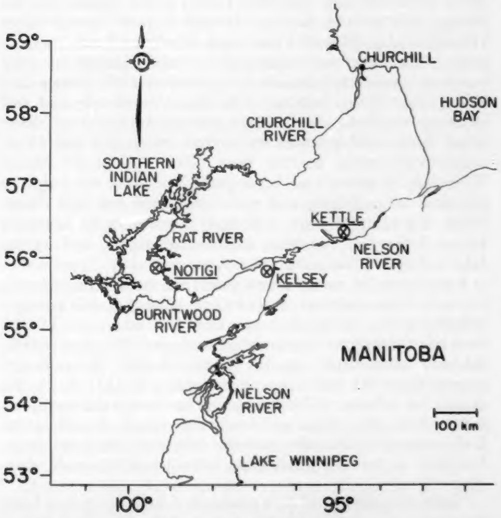

FIG. 1. The field area.

TABLE 1. List of water samples and sampling localities, with pH and conductivity data. ("n.d." means no data.)

Sample no.	Sampling locality	Backwater (BW) or main-stem (MS)	pH	Conductivity (μS/cm)	Comments
Not-1	Notigi Reservoir, east side	BW	7.50	119	Sampled 0.5 yr after impoundment.
Not-2	Notigi Reservoir, west side	MS	7.65	139	Sampled 0.5 yr after impoundment.
Ket-1	Kettle Reservoir	BW	8.00	280	Sampled 3 yr after impoundment.
Ket-2	Kettle Reservoir	MS	8.10	355	Sampled 3 yr after impoundment.
Kel-1	Kelsey Reservoir	BW	8.05	205	Sampled 14 yr after impoundment.
Kel-2	Kelsey Reservoir	MS	8.10	365	Sampled 14 yr after impoundment.
SIL-1	Stream entering South Bay, Southern Indian Lake	BW	7.40	n.d.	Sluggish, humus-rich brown water. Many rooted plants.
SIL-2	Mouth of stream entering South Bay, Southern Indian Lake	BW	7.55	n.d.	Humus-rich brown water. Many rooted plants.
SIL-3	South Bay, Southern Indian Lake	BW	8.55	171	Contained suspended clay and carbonate minerals eroded from glacial varve deposit on shore.
SIL-4	Center of South Bay, Southern Indian Lake	BW	8.20	155	
SIL-5	Stream entering Sand Hill Bay, Southern Indian Lake	BW	7.90	n.d.	Sluggish, humus-rich brown water.
SIL-6	Mouth of stream entering Sand Hill Bay, Southern Indian Lake	BW	8.10	n.d.	Many rooted plants.
SIL-7	Center of Sand Hill Bay, Southern Indian Lake	BW	8.00	116	
SIL-8	Northeast sector of Southern Indian Lake, near Missi Rapids	MS	8.15	99	

Notigi Reservoir, the Nelson River flows through the Kelsey and Kettle reservoirs (in that order), and the Churchill River flows through Southern Indian Lake. Originally, the Notigi, Kettle, and Kelsey reservoirs were natural lakes (Notigi Lake, Moose Lake, and Cauchon Lake, respectively), but they were enlarged by impoundment of river water to generate hydroelectric power. At the Kettle and Kelsey reservoirs, impoundment was completed, and full capacity reached, after a 2-yr transition period of rising water levels; stable water levels were reached 3 and 14 yr, respectively, prior to the time of sampling. At Notigi Reservoir, flooding had been going on for 6 mo prior to the time of sampling, and the water level was still rising. When the samples were collected, the waters of Southern Indian Lake had not been impounded at all, and so the lake was in a "baseline" condition.[1]

Each body of water investigated can be subdivided into (1) relatively stagnant "backwater" bays that are strongly influenced by local drainage and (in the case of the reservoirs) by recently inundated land, and (2) more rapidly flushed "main-stem" regions whose waters more nearly approximate the inflowing river water (Baxter 1977). To assess the effects of impoundment or local drainage, we sampled the main-stem and backwater zones of each water body separately, and observed the differences between them. Included in the backwater class were a pair of small, sluggish brown-water streams flowing into semi-isolated embayments of Southern Indian Lake. At Kettle Reservoir, paired observations of backwater and main-stem water had been made at different times of the year during 1972 and 1973 (~1–2 yr after impoundment) by Cleugh (1974) and by Hecky and Harper (1974), and relevant data from these studies are presented here.

The field area is characterized by low topographic relief, spruce (*Picea mariana*)-dominated boreal forest, sub-Arctic climate, and podzolic soil. The region lies on the Precambrian Shield, but the bedrock is largely covered with calcareous glacial drift.

FIELD WORK

The water samples and field data were collected during September 10–13, 1974. Water samples were taken with a polyvinyl chloride (PVC) van Dorn bottle at a depth of 2 m and transferred to PVC bottles, or were collected by hand with polyethylene jugs. Temperature, conductivity, and light transmission profiles of the water column were made by means of a Whitney temperature-conductivity probe and a Martek horizontal-beam transmissometer with a 25 cm folded light path. Light transmission, expressed as percent transmittance (T), was converted to the beam attenuation coefficient (α) for a 1 m light path, using the equation $\alpha = \ln (T^{-4})$. A 25 cm black and white Secchi disc was used to determine attenuation of image-forming light, and the vertical extinction coefficient (k) of photosynthetically active light was determined by measuring underwater irradiance and surface irradiance (in air) with a Lambda Instruments quantum meter and underwater quantum sensor.

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[1] Since completion of this research, Southern Indian Lake has been expanded by impoundment of the Churchill River.

Laboratory Work

Water samples were passed through ~1 μm glass fiber filters (Whatman GF/C) and then analyzed for major elements, including total dissolved phosphorus (TDP), total dissolved nitrogen (TDN), dissolved organic carbon (DOC), and iron (Fe), and for chlorophyll-*a* content, by the methods of Stainton et al. (1974). Color, which is often used as an indicator of humic matter (Christman and Ghassemi 1966) was measured with a Hellige Aquatestor. Maximum possible concentrations of dissolved inorganic phosphate–phosphorus (PO_4-P) were estimated by the $^{32}PO_4$ radiobioassay method described by Rigler (1966) and Levine and Schindler (1979), using unfiltered water. Primary productivity, defined as the rate at which inorganic carbon is transformed to particulate organic carbon by phytoplankton at optimum light intensity, was measured in a light-gradient incubator (Shearer 1976) using the ^{14}C liquid scintillation techniques described by Schindler (1966), Schindler et al. (1972), and Fee (1973). The results were expressed as mg $C \cdot m^{-3} \cdot h^{-1}$.

Water used for the study of dissolved or dispersed humic complexes was passed through 0.45-μm Millipore filters which had been pre-cleaned with 0.001 mol/L HCl and hot (90–100°C) deionized distilled water (DDW) and leached with 1 L of DDW at room temperature, and the pH of the filtrate was determined with a Corning-12 pH meter. A portion of each sample was then dialyzed in a Pope multiple dialyzer using cellulose dialysis tubing with a 4.8-nm pore diameter nominally capable of retaining substances of molecular weight $\geq$12 000. Known volumes of both the dialyzed and the undialyzed portions were freeze-dried in a Virtis freeze-dryer, and the nonvolatile residue was weighed. The freeze-dry residues of dialyzed and undialyzed water — defined as the "colloidal" (or "nondialyzable") and "total" dissolved solids, respectively — were analyzed by chemical and spectrophotometric techniques, and the data were calculated on the basis of unit volume of original water sample as well as unit weight of solid residue.

To determine the chemical composition of the freeze-dry residues, we redissolved weighed quantities of residue in DDW and made them up to a known volume, and the solutions were analyzed in duplicate or triplicate. Organic carbon (org. C) was determined with a Beckman-915 analyzer. Aliquots of the solutions were wet-ashed by ultraviolet photo-oxidation (Stainton et al. 1974), using 5 mL of sample solution + 20 mL of 0.33% H_2SO_4 + 10 drops of 30% H_2O_2, and were analyzed for phosphorus (P) by the molybdate method (Stainton et al. 1974), for iron (Fe) by the *o*-phenanthroline method (Sandell 1959) (or by atomic absorption if the sample was relatively Fe-rich), for aluminum (Al) by the aluminon method (Sandell 1959), for calcium (Ca) by means of a Perkin-Elmer-403 atomic absorption spectrophotometer, and for nitrogen (N) by the chloramine-T procedure (Banoub 1972).

Weighed portions of freeze-dry residue were dissolved in known volumes of 0.025 mol/L $Na_2B_4O_7$ buffer (pH 9.15) (giving concentrations of ~0.1–4.83 mg/mL) to maintain a constant ambient pH and ionic environment for all samples, and the ultraviolet (UV) and visible absorption spectra of the solutions were recorded with a Cary-14 spectrophotometer. Absorbance (A_λ) was then measured at selected wavelengths (λ), and the absorbance ratio A_{465nm}/A_{665nm} was used to determine the degree of "humic," as opposed to "fulvic," character of the humic matter (Schnitzer 1971; Chen et al. 1977). A_{465nm} and A_{665nm} represent a monotonic absorption band extending across the entire UV-visible range. Another parameter designated as A_{265nm} (peak) was used to represent the intensity of a discrete absorption peak superimposed on this otherwise featureless band (Jackson et al. 1980).

The light-absorption parameter A_{465nm} was used to estimate the relative abundance of humic matter in each sample (the humic content of the dissolved solids being represented by the A_{465nm} value for 1 mg of freeze-dry residue dissolved in 1 mL of borate buffer). A_{465nm} is widely used for semiquantitative determination of humic or fulvic acid in "solution" (Schnitzer 1971), but some caution is required in the interpretation of it, because (1) absorbance is a function of extinction coefficient as well as concentration, and (2) scattering of light by various dispersed colloids could contribute to the "absorbance" readings. The extinction coefficient varies with factors such as molecular size and structure, functional group content, and the nature and abundance of complexed substances.

The freeze-dry residues were further characterized by gel filtration, whereby components were separated approximately according to molecular size. Five-mL aliquots of the borate solutions were fractionated on a Pharmacia Sephadex G-25 column 25 cm in diameter using 0.025 mol/L $Na_2B_4O_7$ as the eluant, and 5-mL fractions were taken automatically every 3 min. The fractions were analyzed chemically and spectrophotometrically as outlined above.

Infrared (IR) absorption spectra of the freeze-dry residues of dialyzed water samples were recorded by means of a Perkin-Elmer-467 IR spectrophotometer employing KBr pellets. Dialyzed samples were used to minimize interference due to inorganic salts, even though some lower molecular weight humic matter may have been lost during dialysis. A portion (0.38–1.20 mg) of each sample was weighed out with a Cahn electrobalance, mixed with 400 mg of desiccated IR-grade KBr in a ball mill, and pressed into a pellet. KBr reference pellets were used to cancel out the spectrum of hygroscopic water in the KBr of the sample pellet. The absorbance values and frequencies (i.e. peak positions) of major IR absorption bands representing H-bonded "polymeric" hydroxyl (OH) and ionized carboxyl (COO^-) groups were measured. To verify the identity of the COO^- bands and to test the stability of carboxyl-metal bonding, portions of a selected backwater sample — sample SIL-2 (Table 1) — were treated with HCl solutions and then analyzed spectrophotometrically and chemically together with an untreated control. The purpose of acidification was to convert COO^- groups to COOH by displacement of metal ions. The acid treatment involved exposure to (1) 0.5 mol/L HCl at room temperature for about 16.5 h and (2) boiling 6 mol/L HCl for about 30 min; the control was dissolved in H_2O at room temperature. The HCl and control solutions were dialyzed and freeze-dried, and the IR spectra of the freeze-dry residues were recorded. The KBr pellets containing the samples, together with KBr blank pellets, were then analyzed for Fe, Al, and org. C.

Relationships between the various chemical, physical, and biological data were tested by regression analysis involving computation of regression lines, correlation coeffi-

TABLE 2. Primary productivity and average concentrations of total dissolved phosphorus and nitrogen and the maximum possible dissolved inorganic phosphate concentrations (determined by radiobioassay) in the lake and reservoir waters. For explanation of sample designations, see Table 1.[a] ("n.d." means no data.)

Sample	Primary productivity ($mgC \cdot m^{-3} \cdot h^{-1}$)	TDP	TDN	PO_4-P	% PO_4-P in TDP
		(μmol/L)			
Not-1 (BW)	13.1	1.23	42.1	0.039	3.2
Not-2 (MS)	n.d.	2.39	49.3	0.45	19
Ket-1 (BW)	8.6	5.10	42.8	0.0068	0.13
Ket-2 (MS)	15.8	1.32	27.8	0.087	6.6
Kel-1 (BW)	14.9	0.39	31.4	0.001	0.3
Kel-2 (MS)	15.1	0.42	28.6	0.0058	1.4
SIL-3 (BW)	3.9	0.42	21.4	n.d.	n.d.
SIL-4 (BW)	4.3	0.36	21.4	0.017	4.7
SIL-7 (BW)	3.1	n.d.	n.d.	n.d.	n.d.
SIL-8 (MS)	17.4	0.32	24.3	0.065	20

[a] "Not" = Notigi Reservoir; "Ket" = Kettle Reservoir; "Kel" = Kelsey Reservoir; "SIL" = Southern Indian Lake. "BW" and "MS" mean backwater and main-stem, respectively.

cients (r), and significance probabilities (P). A correlation is defined as "significant" if $P \leq 0.05$.

Results and Discussion

GENERAL CHARACTERISTICS OF THE WATER

All water samples were weakly alkaline and had moderately high levels of dissolved salts (Table 1), reflecting the influence of calcareous glacial drift. The backwater regions had (1) generally higher concentrations of dissolved org. C and higher ratios of organic to inorganic dissolved solids (i.e. higher concentrations of org. C and N in their freeze-dry residues), (2) lower PO_4-P concentrations and lower PO_4-P:TDP ratios, and (3) lower levels of primary productivity than did the corresponding main-stem regions (Tables 2 and 3). Some of the backwaters — especially streams and mouths of streams — had a distinctly brownish coloration which may be ascribed to predominantly allochthonous humic matter. Presumably this humic matter had a greater tendency to accumulate in poorly flushed, semi-isolated bays than in main-stem waters. The systematic differences between backwater and main-stem environments imply that alteration of water properties in the backwater regions as a result of local drainage and low rates of water renewal has an adverse effect on primary production in both the lake and the reservoirs.

RELATIONSHIP BETWEEN PRIMARY PROCUCTIVITY AND WATER CHEMISTRY: THE IMPORTANCE OF ORGANIC MATTER AND IRON

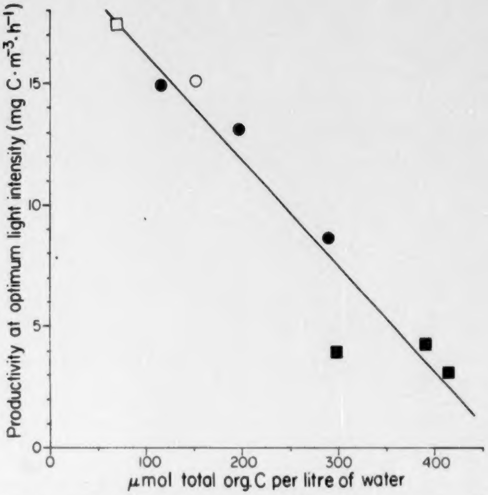

FIG. 2. Relationship between primary productivity and concentration of total dissolved organic carbon in the lake and reservoir waters ($r = -0.961$; $P < 0.001$). Explanation of symbols — reservoirs: backwater, ●; main stem, ○; Southern Indian Lake: backwater, ■; main stem: □.

In the light of current theories of eutrophication Vollenweider 1968; Schindler 1974, 1977), the depressed levels of primary productivity in backwater bays with respect to main-stem localities might seem at first sight to be readily explained by the low concentrations of dissolved PO_4-P in the backwater environments. Another seemingly plausible hypothesis is that organic matter in backwater regions depressed algal productivity by reducing the availability of light or by lowering the pH of the water. However, more detailed examination of our data (Tables 1–7) with the aid of regression analyses for testing the relationships between productivity and various physicochemical properties of the water (Table 8) failed to support these interpretations. We found that primary productivity was strongly correlated with organic matter and iron but not with phosphorus, light, or pH.

Primary productivity in both natural and impounded waters showed a highly significant *inverse* correlation with the total org. C concentration of the water (Fig. 2; Tables 2, 3, and 8) and significant, though weaker, inverse correlations with the Fe and org. C content of the colloidal dissolved solids and the colloidal Fe and N (but not the colloidal org. C) concentrations of the water (Fig. 3A and B; Tables 2, 3, and 8). In each plot shown in Fig. 2 and 3, the data for all the samples — lake as well as reservoir waters, and main-stem as well as backwater samples — cluster around the same trend line, indicating that the observed relationship prevails throughout the field area and is not restricted to a particular environment or locality. On the

TABLE 3. The average chemical composition of (A) dialyzed and undialyzed filtered water samples and (B) the dissolved solids isolated from these samples by freeze-drying, together with the yield of freeze-dry residue per unit volume of water. The data in Table 3A were computed from the data in Table 3B. For explanation of sample designations, see Table 1.[a] ("n.d." means no data.)

A	Undialyzed					Dialyzed				
Sample	P	Fe	Al (μmol/L)	org. C	N	P	Fe	Al (μmol/L)	org. C	N
Not-1 (BW)	0.381	0.270	0.292	196	14.5	0.132	0.231	0.550	158	8.22
Not-2 (MS)	0.114	0.638	5.64	117	5.29	0.0894	0.257	3.10	89.3	4.52
Ket-1 (BW)	0.733	0.445	19.0	289	15.2	0.242	0.338	3.47	214	12.8
Ket-2 (MS)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Kel-1 (BW)	0.104	0.167	4.59	114	4.62	0.187	0.0929	2.55	243	9.62
Kel-2 (MS)	0.140	0.224	13.0	152	7.26	0.0414	0.0642	3.53	53.4	3.70
SIL-1 (BW)	0.403	2.83	15.5	710	22.6	0.326	2.26	1.64	337	13.6
SIL-2 (BW)	0.403	2.77	11.8	698	21.2	0.343	1.60	1.21	377	15.8
SIL-3 (BW)	0.118	0.371	7.73	298	7.40	0.212	0.687	3.92	239	17.3
SIL-4 (BW)	0.128	0.123	2.62	390	8.89	0.0408	0.145	1.34	99.7	9.16
SIL-5 (BW)	0.334	1.21	11.0	329	19.7	0.193	0.950	2.05	408	16.1
SIL-6 (BW)	0.433	1.39	15.7	721	21.8	0.185	0.969	5.37	373	21.4
SIL-7 (BW)	0.111	0.559	4.06	416	18.6	0.182	0.509	4.24	276	12.2
SIL-8 (MS)	0.0702	0.149	4.38	69.5	2.50	0.553	0.0843	1.39	41.7	4.82

B	Undialyzed						Dialyzed					
Sample	Freeze-dry residue (mg/L)	P	Fe	Al (μmol/g)	org. C	N	Freeze-dry residue (mg/L)	P	Fe	Al (μmol/g)	org. C	N
Not-1 (BW)	40.0	9.52	6.76	7.31	4895	363	11	11.7	20.5	50.0	14 100	731
Not-2 (MS)	49.88	2.29	12.8	113	2350	106	6.0	14.9	42.9	517	14 900	754
Ket-1 (BW)	135.8	5.40	3.28	140	2130	112	16.6	14.6	20.4	209	12 900	768
Ket-2 (MS)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Kel-1 (BW)	86.8	1.20	1.92	52.9	1317	53.2	19.6	9.54	4.75	130	12 400	491
Kel-2 (MS)	205.7	0.679	1.09	63.3	737	35.3	7.1	5.85	9.06	497	7 535	523
SIL-1 (BW)	131.2	3.07	21.6	118	5410	172	21.8	15.0	104	75.3	15 500	625
SIL-2 (BW)	131.4	3.07	21.1	89.8	5310	161	24.5	14.0	65.4	49.5	15 400	643
SIL-3 (BW)	104.5	1.13	3.55	74.0	2850	70.8	17.8	11.9	38.6	220	13 400	969
SIL-4 (BW)	81.56	1.57	1.51	32.1	4780	109	7.38	5.53	19.6	182	13 500	1240
SIL-5 (BW)	112.8	2.96	10.7	97.6	2920	175	25.0	7.70	38.0	82.1	16 300	644
SIL-6 (BW)	135.3	3.20	10.3	116	5330	161	24.2	7.66	40.0	222	15 400	885
SIL-7 (BW)	71.8	1.53	7.79	56.5	5800	259	19.0	9.56	26.8	223	14 500	643
SIL-8 (MS)	36.8	1.91	4.05	119	1890	68	6.6	8.40	12.8	211	6 340	732

[a] "Not" = Notigi Reservoir; "Ket" = Kettle Reservoir; "Kel" = Kelsey Reservoir; "SIL" = Southern Indian Lake (or influent stream). "BW" and "MS" mean backwater and main-stem, respectively.

other hand, productivity failed to correlate significantly with total or colloidal dissolved P, PO_4-P, total dissolved N, Fe, or Al, colloidal dissolved Al, or pH, or with any of the light attenuation parameters (k, a, and Secchi disc value) (Tables 1–4, and 8). It would seem, then, that the photosynthetic activities of phytoplankton in the bodies of water investigated are depressed in the presence of relatively high concentrations of dissolved organic matter and high molecular weight nitrogenous organic-Fe complexes or colloidal hydrated ferric oxide (FeOOH) peptized by adsorbed organic matter; but this phenomenon evidently cannot be ascribed to the scavenging of phosphate by these ferric complexes nor to absorption or scattering of light or excessive lowering of the pH of the water (which is well buffered in any case). Before proposing an hypothesis to explain these results, let us examine in greater detail the nature of the organic matter and iron and their relationship with primary productivity.

THE NATURE OF THE ORGANIC-IRON COMPLEXES IN RELATION TO THE MECHANISM OF TROPHIC DEPRESSION

The preponderance of humic components in the dissolved organic matter — The organic matter dissolved or dispersed in the lake, reservoir, and stream water appeared to consist chiefly of humic substances, as indicated by the UV-visible and IR absorption spectra (Fig. 4A and B), the Sephadex data (Fig. 5), and

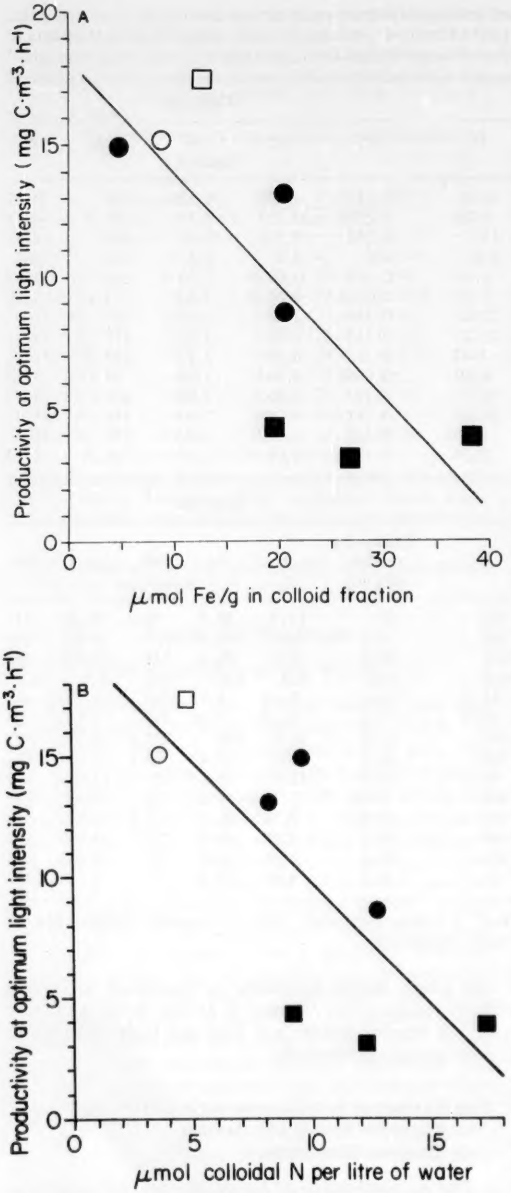

FIG. 3. Relationship between primary productivity and (A) concentration of iron in freeze-dried colloidal dissolved solids ($r = -0.793$; $P < 0.02$, >0.01) and (B) concentration of colloidal dissolved nitrogen in the water ($r = -0.768$; $P < 0.02$, >0.01). Explanation of symbols — reservoirs: backwater, ●; main stem, ○; Southern Indian Lake: backwater, ■; main stem, □.

TABLE 4. Vertical extinction coefficient (k), beam attenuation coefficient (α), Secchi disc reading, and chlorophyll-*a* content of the water. For explanation of sample designations, see Table 1.[a]

Sample	k	α	Secchi disc (m)	Chlorophyll-*a* (μg/L)
Not-1 (BW)	1.33	1.9	2.4	4.2
Not-2 (MS)	1.15	2.3	1.7	1.4
Ket-1 (BW)	1.05	2.0	2.1	6.0
Ket-2 (MS)	0.96	6.9	0.8	6.7
Kel-1 (BW)	0.92	3.3	1.8	4.7
Kel-2 (MS)	n.d.	7.0	0.8	5.0
SIL-3 (BW)	1.3	6.9	0.7	1.9
SIL-4 (BW)	0.60	1.5	1.6	1.7
SIL-7 (BW)	1.0	1.6	1.9	2.3
SIL-8 (MS)	0.69	1.5	2.6	4.7

[a] "Not" = Notigi Reservoir; "Ket" = Kettle Reservoir; "Kel" = Kelsey Reservoir; "SIL" = Southern Indian Lake. "BW" and "MS" mean backwater and main-stem, respectively

the brownish coloration of the dissolved solids. The spectra of all samples are similar to the spectra of humic matter extracted from soil and lake mud (Schnitzer 1965, 1971; Stevenson and Goh 1971) and are almost identical to each other qualitatively. The total and colloidal org. C and Fe correlated significantly with light absorption at 465 nm (Table 9), lending credibility to the conclusion that much of the organic matter consisted of humic substances associated with Fe. The brownish color of the streams draining the field area (Table 1) suggests that at least a major part of this humic matter was leached or eroded from local soils. The A_{465nm}/A_{665nm} ratios of the samples were relatively high (≥ 6.0) (Table 5), showing that most of the humic matter belonged to the "fulvic acid" category (Schnitzer 1971; Chen et al. 1977), as is generally the case with humic substances dissolved in natural waters (Black and Christman 1963; Ghassemi and Christman 1968; Reuter and Perdue 1972).

Gel filtration — Gel filtration provided additional evidence that the organic matter was predominantly humic. Thus, the Sephadex elution patterns, as illustrated in Fig. 5, revealed that the dissolved organic matter strongly absorbed UV-visible radiation, was concentrated in the higher molecular size fractions (near the "void" volume), and accounts for the UV-visible spectra of the water. In the example shown (representing local stream water draining into Southern Indian Lake), most of the dissolved P was associated with the two highest molecular weight Fe fractions, and probably represented phosphates bound to FeOOH and Fe^{3+} complexed with humic matter; but no free ortho-PO_4 was detected. The Sephadex data suggest that the colloidal fractions of the dissolved solids are composed primarily of humic matter complexed with inorganic species such as FeOOH and Fe^{3+}.

Infrared spectra — The IR spectra of the colloidal dissolved solids (Fig. 4B; Table 6) yielded additional information on the nature of the humic-iron complexes and their role in the limitation of primary productivity. The spectra demonstrate that the major functional groups of the "dissolved" colloids were H-bonded "polymeric" hydroxyl (OH) groups, whose stretching vibrations are represented by the band at 3300–3400 cm^{-1}, and ionized carboxyl (COO^-) groups, whose antisymmetric and symmetric stretching frequencies are represented by the bands at approximately 1600 cm^{-1} and 1400 cm^{-1}, respectively (Bellamy 1958). The band at 1600 cm^{-1}, however, may be due to aromatic C=C and H-bonded or conjugated carbonyl groups as well as COO^- groups (Schnitzer 1971; Stevenson and Goh 1971). In all of the samples examined, undissociated carboxyl (COOH) groups are relatively unimportant, as demonstrated by the fact that the COOH band at about 1700 cm^{-1} is only a small shoulder on the flank of the 1600 cm^{-1} band. Thus, the humic substances in their native state are mainly in the form of complexes or salts.

Strong binding of Fe and Al oxides by humic COO^- groups — Acid treatments caused small but measurable increases in the intensity of the COOH band with respect to the two COO^- bands, the effect being more pronounced, as expected, for hot 6 mol/L HCl than for cold 0.5 mol/L HCl (Table 7; Fig. 4C). These results tend to confirm our assignment of the 1600 cm^{-1} and 1400 cm^{-1} bands to COO^- groups, but the effect of acidification was much less pronounced than might be anticipated, suggesting that most of the carboxyl–metal bonds were exceedingly strong and predominantly covalent. Chemical analysis furnished additional support for this conclusion. The concentrations of org. C, Fe, and Al in the nondialyzable fraction *increased* with increasingly rigorous acid treatment (Table 7), presumably owing to accumulation of acid-resistant organic complexes of Fe and Al accompanied by loss of the more hydrolyzable or acid-soluble constituents such as the unidentified substances (possibly compounds with ether linkages, like polysaccharides) which yielded the C-O and =C-O absorption bands at 1000–1100 cm^{-1} and approximately 1250 cm^{-1}, respectively (Fig. 4C) (Stevenson and Goh 1971). It would seem that the nondialyzable Fe and Al were largely in the form of extremely stable, refractory high molecular weight humic complexes in which carboxyl

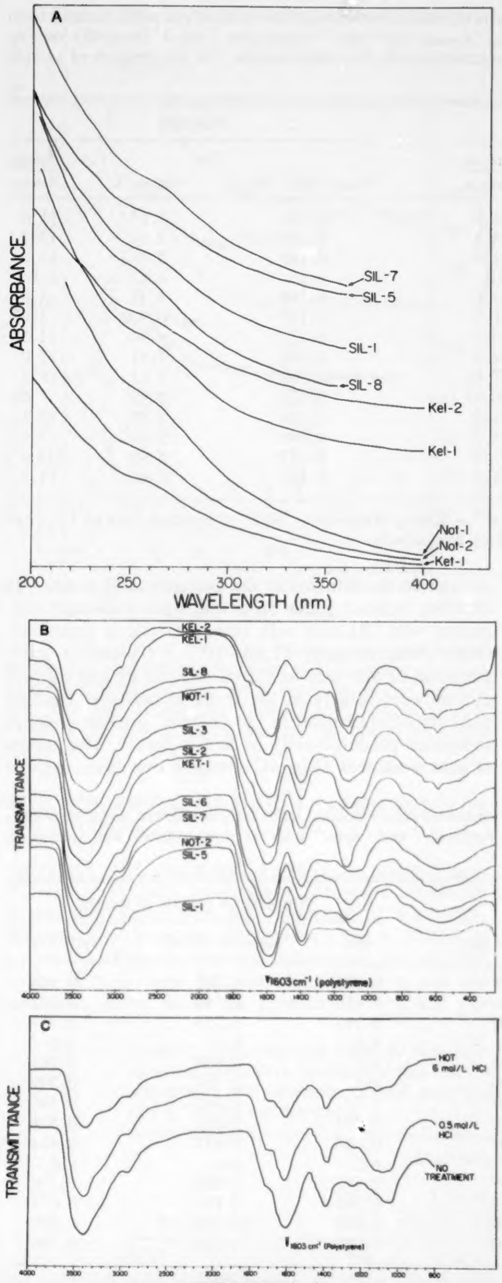

FIG. 4. Absorption spectra of dissolved substances. For explanation of sample designations, see Table 1. ("Not" = Notigi; "Ket" = Kettle; "Kel" = Kelsey; "SIL" = Southern Indian Lake [or influent stream].) A, Ultraviolet spectra of sodium borate solutions of total dissolved solids isolated from undialyzed water samples by freeze-drying; B, Infrared spectra of colloidal dissolved solids isolated from dialyzed water samples by freeze-drying; C, Infrared spectra of acid-treated colloidal dissolved solids, and untreated control, from Southern Indian Lake backwater sample SIL-2.

TABLE 5. Data from visible absorption spectra obtained by analysis of sodium borate solutions of dissolved solids isolated from dialyzed and undialyzed filtered water samples by freeze-drying. "$A_{465nm} \cdot mg^{-1} \cdot mL^{-1}$" represents 1 mg of freeze-dry residue redissolved in 1 mL of borate buffer; "A_{465nm}/L" represents concentration in the water sample. For explanation of sample designations, see Table 1.[a] ("n.d." means no data.)

Sample	Undialyzed			Dialyzed		
	$A_{465nm} \cdot mg^{-1} \cdot mL^{-1}$	A_{465nm}/L	$\frac{A_{465nm}}{A_{665nm}}$	$A_{465nm} \cdot mg^{-1} \cdot mL^{-1}$	A_{465nm}/L	$\frac{A_{465nm}}{A_{665nm}}$
Not-1 (BW)	0.0910	3.64	14.8	0.324	3.65	11.6
Not-2 (MS)	0.0901	4.49	14.5	0.354	2.12	12.3
Ket-1 (BW)	0.0395	5.36	12.0	0.186	3.08	13.4
Ket-2 (MS)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Kel-1 (BW)	0.0351	3.05	35.8	0.169	3.31	13.6
Kel-2 (MS)	0.00632	1.30	61.0	0.127	0.900	4.07
SIL-1 (BW)	0.0804	10.6	10.7	0.319	6.94	12.5
SIL-2 (BW)	0.0710	9.33	14.0	0.323	7.91	12.0
SIL-3 (BW)	0.0184	1.92	7.51	0.119	2.12	15.8
SIL-4 (BW)	0.0112	0.914	6.03	0.122	0.901	7.09
SIL-5 (BW)	0.0941	10.6	15.0	0.363	9.08	12.1
SIL-6 (BW)	0.0969	13.1	14.3	0.388	9.40	12.9
SIL-7 (BW)	0.0587	4.21	15.4	0.315	5.99	13.4
SIL-8 (MS)	0.0276	1.01	14.5	0.157	1.03	14.7

[a] "Not" = Notigi Reservoir; "Ket" = Kettle Reservoir; "Kel" = Kelsey Reservoir; "SIL" = Southern Indian Lake (or influent stream). "BW" and "MS" mean backwater and main-stem, respectively.

groups played a major metal-binding role (Kříbek et al. 1977). Metals bound in this summer could well be unavailable to organisms.

Assignment of the two COO⁻ bands to humic matter is consistent with the observation that the band intensities correlate significantly with A_{465nm} and org. C (Table 10). The intensity of the OH band, however, is more weakly correlated with A_{465nm} and org. C, suggesting that the OH groups belong to inorganic as well as organic constituents of the nondialyzable solutes. In contrast, nondialyzable Fe is much more strongly correlated with OH than with antisymmetric or symmetric COO⁻ band intensity (Table 10). A reasonable interpretation of our data would be that the Fe and the OH groups were largely in the form of colloidal FeOOH particles firmly bound to "protective" organic coatings composed predominantly of humic matter. The results of acid treatment (Fig. 4C) suggest that these organic

TABLE 6. Data from infrared absorption spectra for "colloidal" dissolved solids isolated from dialyzed filtered water by freeze-drying. For explanation of sample designations, see Table 1.[a] "Antisym." and "sym." refer to antisymmetric and symmetric stretching vibrations, respectively. ("n.d." means no data.)

Sample	Frequency (cm^{-1})			Absorbance per mg of sample		
	OH	Antisym. COO⁻	Sym. COO⁻	OH	Antisym. COO⁻	Sym. COO⁻
Not-1 (BW)	3329	1594	1408	0.675	0.785	0.534
Not-2 (MS)	3370	1604	1404	0.676	0.740	0.492
Ket-1 (BW)	3362	1604	1405	0.793	0.755	0.457
Ket-2 (MS)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Kel-1 (BW)	3299	1584	1409	n.d.	0.666	0.484
Kel-2 (MS)	3289	1626	1409	n.d.	0.325	0.209
SIL-1 (BW)	3409	1609	1404	1.32	0.961	0.566
SIL-2 (BW)	3359	1599	1409	0.784	0.811	0.508
SIL-3 (BW)	3349	1599	1407	0.606	0.631	0.434
SIL-4 (BW)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
SIL-5 (BW)	3389	1598	1407	0.842	0.800	0.538
SIL-6 (BW)	3369	1600	1409	0.802	0.881	0.671
SIL-7 (BW)	3369	1609	1409	0.692	0.713	0.469
SIL-8 (MS)	3309	1612	1402	0.668	0.623	0.396

[a] "Not" = Notigi Reservoir; "Ket" = Kettle Reservoir; "Kel" = Kelsey Reservoir; "SIL" = Southern Indian Lake (or influent stream). "BW" and "MS" mean backwater and main-stem, respectively.

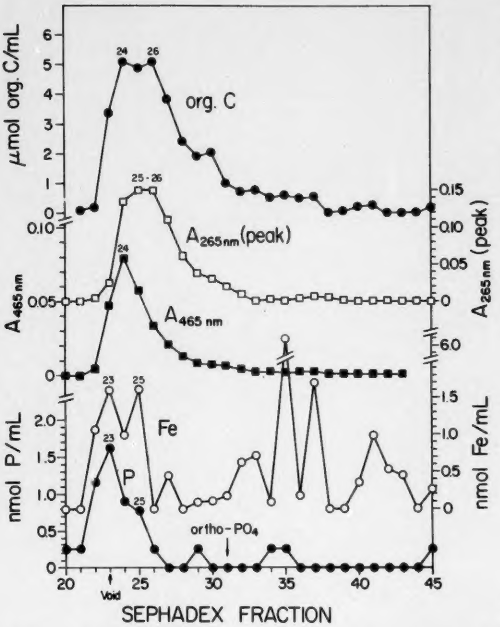

FIG. 5. Distribution of organic carbon, iron, phosphorus, and spectral properties in Sephadex G-25 fractions of borate solution of total dissolved solids from the stream entering Sand Hill Bay of Southern Indian Lake (sample SIL-5). Numbers on peaks refer to corresponding Sephadex fractions.

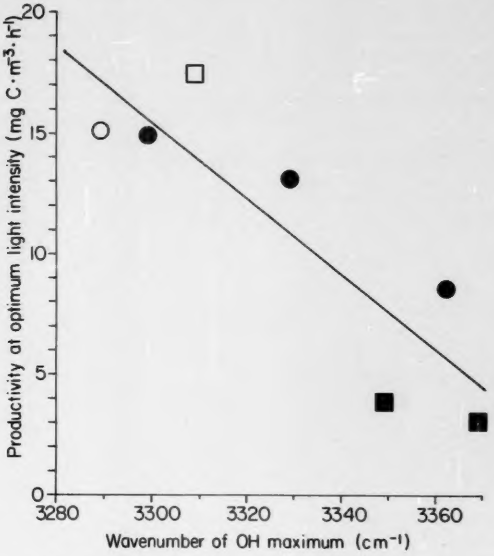

FIG. 6. Relationship between primary productivity and frequency (position) of infrared absorption band for stretching vibration of H-bonded "polymeric" OH groups in colloidal dissolved solids isolated from dialyzed water samples by freeze-drying ($r = -0.873$; $P < 0.02$, >0.01). Explanation of symbols — reservoirs: backwater, ●; main stem, ○; Southern Indian Lake: backwater, ■; main stem, □.

layers were fixed to the FeOOH surfaces largely by -COO-Fe bonds.

Relevance of complexed FeOOH to primary productivity — Primary productivity showed a significant inverse correlation with the frequency of the 3300–3400 cm^{-1} IR band for OH groups (Fig. 6; Tables 2, 6, and 8). This relationship holds true for all four bodies of water and for both the main-stem and the backwater zones. However, productivity was not significantly related to the frequencies of the COO$^-$ bands, although productivity in *backwater* regions did tend to correlate inversely with the 1600 cm^{-1} band frequency (Tables 2 and 6). The frequency of the OH band also correlates strongly with the Fe content of the nondialyzable material, and significantly though more weakly with the concentrations of org. C and $A_{465\text{nm}}$ units (Fig. 7; Tables 3, 6, and 10). Al, however, gave no significant correlation (Tables 3 and 10). These observations probably indicate that the OH groups of the FeOOH give a higher band frequency than do the

TABLE 7. Chemical and infrared-absorption data for acid-treated and untreated "colloidal" dissolved solids from Southern Indian Lake backwater sample SIL-2 (see Table 1). The treated subsamples and untreated control were dialyzed and freeze-dried before being analyzed. ("n.d." means not detected.)

	Absorbance ratio					
Reagent used	COOH / OH	COOH / Antisym. COO⁻	COOH / Sym. COO⁻	org. C	Fe (µmol/g)	Al
H$_2$O	0.358	0.424	0.656	34 700	n.d.	570
0.5 mol/L HCl	0.361	0.517	0.774	33 300	920	1600
Hot 6 mol/L HCl	0.547	0.649	0.792	105 000	1850	2100

TABLE 8. Correlation matrix showing relationship between primary productivity and various physicochemical parameters of the water and dissolved solids in backwater and main-stem regions of the reservoirs and Southern Indian Lake. "n.s." means not significant.[a] "Antisym." and "sym." refer to antisymmetric and symmetric stretching vibrations, respectively. Other abbreviations are explained in sections on field work and laboratory work.

Chemical and physical properties of the water			Correlation with productivity	
Type of property or phenomenon measured (and units used)	Treatment of water sample	Parameter or constituent tested	*r*	*P*
Elemental composition of water (μmol/L)	Undialyzed	org. C	−0.961	<0.001
		Fe	−0.580	n.s.
		P	−0.0442	n.s.
		TDP	−0.157	n.s.
		PO_4-P	0.459	n.s.
		N	−0.555	n.s.
		TDN	0.210	n.s.
		Al	0.0105	n.s.
	Dialyzed	org. C	0.0663	n.s.
		Fe	−0.761	<0.05; >0.02
		P	−0.371	n.s.
		N	−0.768	<0.02; >0.01
		Al	−0.436	n.s.
Elemental composition of freeze-dried dissolved solids (μmol/g)	Undialyzed	org. C	−0.653	<0.1; >0.05
		Fe	−0.247	n.s.
		P	0.143	n.s.
		N	−0.210	n.s.
		Al	0.136	n.s.
	Dialyzed	org. C	−0.732	<0.05; >0.02
		Fe	−0.793	<0.02; >0.01
		P	−0.155	n.s.
		N	−0.611	n.s.
		Al	0.114	n.s.
Infrared band frequency (cm^{-1})	Dialyzed	OH	−0.873	<0.02; >0.01
		COO^- (antisym.)	0.0828	n.s.
		COO^- (sym.)	−0.275	n.s.
		COO^- (antisym.) minus COO^- (sym.)	0.130	n.s.
Visible and infrared light absorption (absorbance units/L in water)	Undialyzed	$A_{465\text{nm}}$	−0.213	n.s.
	Dialyzed	$A_{465\text{nm}}$	−0.351	n.s.
		OH	−0.873	<0.1; >0.05
		COO^- (antisym.)	−0.662	n.s.
		COO^- (sym.)	−0.624	n.s.
Visible and infrared light absorption (absorbance units/mg in freeze-dried dissolved solids)	Undialyzed	$A_{465\text{nm}}$	0.0353	n.s.
	Dialyzed	$A_{465\text{nm}}$	−0.0857	n.s.
		OH	0.0805	n.s.
		COO^- (antisym.)	−0.340	n.s.
		COO^- (sym.)	−0.325	n.s.
Light scattering and extinction	Unfiltered	*k*	−0.141	n.s.
		α	0.188	n.s.
		Secchi disc	0.142	n.s.
Hydrogen ion concentration	Undialyzed	pH	−0.373	n.s.

[a] The *P*-value of each "insignificant" correlation in this table is >0.1. Numerical *P*-values are given only if they are "significant" (<0.05) or of doubtful significance (<0.1; >0.05).

phenolic and alcoholic OH groups of the humic substances, thus causing the composite OH band of the sample material to shift to higher frequencies with an increase in the concentration of FeOOH relative to humic matter. Therefore, we postulate that the OH band frequency indirectly measures the FeOOH concentration of the colloidal material, and that FeOOH concentration, in turn, plays a key role in limiting primary productivity. The strong correlation between Fe concentration and OH band intensity (Table 10) lends

TABLE 9. Correlation matrix relating $A_{465\mathrm{nm}}$ to organic carbon and iron in dialyzed and undialyzed filtered water and in total and "colloidal" (undialyzable) freeze-dried dissolved solids (see Table 3). ("n.d." means not determined.)

			Undialyzed				Dialyzed			
			org. C		Fe		org. C		Fe	
			r	P	r	P	r	P	r	P
$A_{465\mathrm{nm}}$	Based on composition of water	Undialyzed	0.772	<0.01; >0.001	0.795	<0.01; >0.001	0.852	<0.001	0.770	<0.01; >0.001
		Dialyzed	n.d.	n.d.	n.d.	n.d.	0.933	<0.001	0.820	<0.001
	Based on composition of dissolved solids	Undialyzed	0.582	<0.05; >0.02	0.870	<0.001	n.d.	n.d.	n.d.	n.d.
		Dialyzed	n.d.	n.d.	n.d.	n.d.	0.700	<0.01; >0.001	0.519	<0.1; >0.05

credence to this interpretation, although another theoretically possible explanation is that the complexing of Fe^{3+} ions by humic matter shifted the IR maximum for phenolic OH groups to higher frequencies by an inductive effect (Bellamy 1958; Nakamoto 1970).

Proposed mechanism of trophic depression—In summary, it would seem that the lake and reservoir waters are less productive at higher concentrations of "dissolved" organic matter, most of which consists of humic substances. The observed effect, which may well be widespread and important in surface waters of northern Manitoba and other regions of the boreal forest zone, is related to the accumulation of Fe in the colloidal component of the dissolved material. This colloidal Fe is probably in the form of FeOOH which has been complexed and peptized by epitaxial films of nitrogenous humic matter. The research data failed, however, to substantiate the hypothesis that the humic-iron complexes depressed primary productivity by re-

TABLE 10. Correlation matrix relating infrared spectral parameters to concentrations of organic carbon, iron, and "humic matter" (as measured by absorption of light at 465 nm) in dialyzed water samples. "n.s." means not significant.[a] "Antisym." and "sym." refer to antisymmetric and symmetric stretching vibrations, respectively. The chemical and IR- and visible-absorption data employed represent concentration in the water (on a volume basis) as well as concentration in the freeze-dried dissolved solids (on a weight basis).

			$A_{465\mathrm{nm}}$		org. C		Fe	
			r	P	r	P	r	P
Based on composition of dissolved solids	IR band position (frequency)	COO^- (antisym.)	-0.255	n.s.	-0.565	<0.1; >0.05	0.0422	n.s.
		COO^-(sym.)	0.124	n.s.	0.317	n.s.	-0.216	n.s.
		OH	0.694	<0.02; >0.01	0.802	<0.01; >0.001	0.881	<0.001
	IR band intensity (absorbance)	COO^- (antisym.)	0.742	<0.01; >0.001	0.784	<0.01; >0.001	0.692	<0.02; >0.01
		COO^- (sym.)	0.768	<0.01; >0.001	0.789	<0.01; >0.001	0.544	<0.1; >0.05
		OH	0.400	n.s.	0.381	n.s.	0.831	<0.01; >0.001
Based on composition of water	IR band intensity (absorbance)	COO^- (antisym.)	0.924	<0.001	0.978	<0.001	0.814	<0.01; >0.001
		COO^- (sym.)	0.931	<0.001	0.970	<0.001	0.788	<0.01; >0.001
		OH	0.862	<0.01; >0.001	0.942	<0.001	0.906	<0.001

[a] The P-value of each "insignificant" correlation in this table is >0.1. Numerical P-values are given only if they are "significant" (<0.05) or of doubtful significance (<0.1; >0.05).

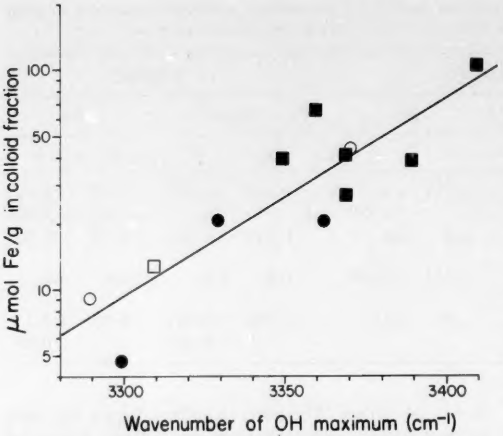

FIG. 7. Relationship between iron and OH groups in colloidal dissolved solids isolated from dialyzed water samples by freeze-drying ($r = 0.881$; $P < 0.001$). Explanation of symbols — reservoirs: backwater, ●; main stem, ○; Southern Indian Lake: backwater, ■; main stem, □.

ducing the availability of phosphate or light or by lowering the pH of the water. What, then, can account for the observed results?

Perhaps the most likely explanation for the apparent depression of primary productivity in the presence of colloidal humic-Fe complexes is that the humic matter renders the Fe and other micronutrients which it sequesters unavailable to phytoplankton. Sakamoto (1971), in a study of other Canadian Shield lakes, reached the same conclusion, and a comparable situation is thought to exist in the case of plants growing on peaty soils (Goodman and Cheshire 1973). Similarly, Giesy (1976) reported that humic acid reduced the availability of Fe to Fe-starved *Scenedesmus* cultures (although the net effect of the humic acid was to stimulate growth of the algae). Possibly Fe fixation by humic matter is responsible for widespread limitation of productivity in the relatively humus-rich waters of the boreal forest zone. Our tentative conclusions do not necessarily conflict with the work of Burk et al. (1932) and D'yakonova (1962), who claimed that humic substances enhance the bio-availability of Fe, thereby stimulating the growth of microorganisms and plants. Whether humic substances stimulate or depress biological activity probably depends on their nature (e.g. average molecular weight) and abundance. Metals bound to the less soluble, higher molecular weight humic substances of soil are thought to be relatively unavailable to plants (Stevenson and Ardakani 1972), and the same principle may well apply to algae. In the present case, possible reasons for inhibition of the biological uptake of metals in the less productive waters include the following: (1) strong, essentially covalent bonding of nutrient metals by humic substances, which thereby interfere with the complexing of these metals by biochemical "carrier" molecules; (2) inability of higher molecular weight humic-metal complexes to pass through cell membranes of algae; (3) steric factors preventing contact between sequestered metals and algal cells or carrier molecules; and (4) scavenging of micronutrients by the FeOOH associated with the humic matter. The greater the concentration of dissolved organic matter, the more efficient the sequestering process.

Nevertheless, our data also suggest that fixation of Fe and other minor metals by humic matter or humic–FeOOH complexes only partially accounts for the unfavorable ecological effect of the organic matter. Primary productivity is more significantly correlated with total dissolved org. C than with any of the parameters associated with colloidal humic–Fe complexes, and is not significantly correlated with A_{465nm}, which supposedly represents the humic component of the organic matter (Table 8). Although the weak correlation between productivity and A_{465nm} may merely reflect the limitations and ambiguity of the A_{465nm} parameter (see section on LABORATORY WORK), our data are consistent with the possibility that nonhumic organic compounds as well as humic matter played a significant role in limiting primary productivity. For instance, toxic compounds such as phenols could have accumulated along with humic matter in the backwater regions. More research is needed to establish the mechanisms of the trophic depression and their relative importance, but the data presented here serve to identify some likely possibilities which merit further study.

SHORT-TERM CHEMICAL ANOMALIES CAUSED BY IMPOUNDMENT, AND THEIR ECOLOGICAL EFFECTS

Analysis of dissolved solids showed that the undialyzed backwater samples from 0.5-yr-old Notigi Reservoir and 3-yr-old Kettle Reservoir had marked chemical anomalies with respect to the rest of the water samples (including samples from lake as well as reservoir stations) (Fig. 8 and 9; Table 3). In contrast, neither the backwater sample from 14-yr-old Kelsey Reservoir nor the main-stem reservoir samples showed such aberrations, demonstrating that the aberrations are short-term effects caused by inundation following impoundment.

Total soluble P in the "normal" samples (all samples except the two aberrant ones) is strongly correlated with A_{465nm} (representing soluble humic matter) and with total soluble Fe, but the Notigi and Kettle backwaters had abnormally high concentrations of P in proportion to A_{465nm} and Fe (Fig. 8A–C). Similarly, total soluble N is correlated with total soluble org. C, but the Notigi backwater had an abnormally high N content (Fig. 8D). In each of these plots, all the "normal" samples cluster about a single regression line,

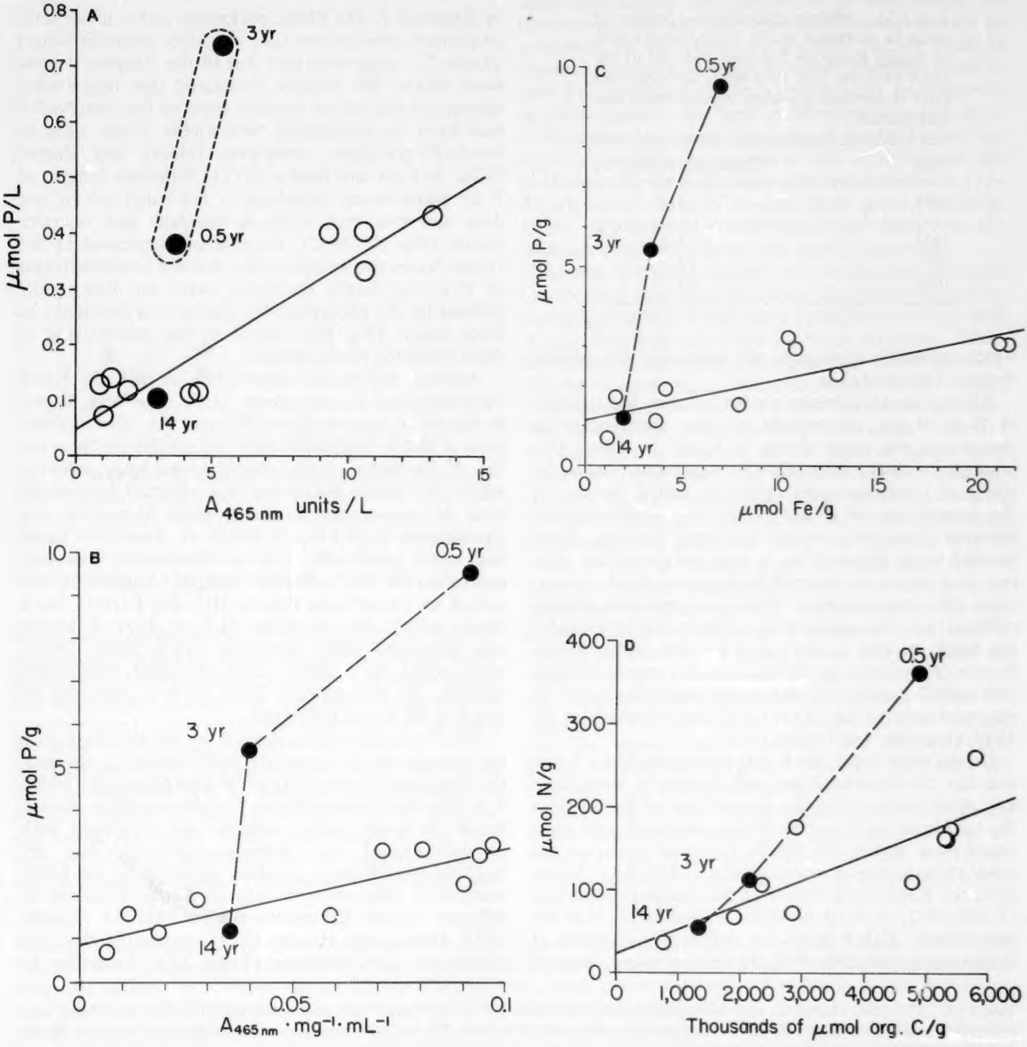

FIG. 8. Relationships between different chemical and spectral properties in the lake, stream, and reservoir waters. A, Total dissolved phosphorus content of water plotted against "humic" content as estimated by absorption of light at 465 nm (for all samples except the 0.5- and 3-yr reservoir backwaters, $r = 0.941$; $P < 0.001$); B, Phosphorus content of total dissolved solids (isolated from undialyzed water by freeze-drying) plotted against "humic" content (estimated by absorption of light at 465 nm) (for all samples except the 0.5- and 3-yr reservoir backwaters, $r = 0.867$; $P < 0.001$); C, Phosphorus content of total dissolved solids plotted against iron content (for all samples except the 0.5- and 3-yr reservoir backwaters, $r = 0.833$; $P < 0.01$, >0.001); D, Nitrogen content of total dissolved solids plotted against organic carbon content (for all samples except the 0.5-yr reservoir backwater, $r = 0.820$; $P < 0.01$, >0.001). NOTE: "$A_{465\mathrm{nm}}$" values represent 1 mg of freeze-dried dissolved solids redissolved in 1 mL of borate buffer. Explanation of symbols — reservoir backwater, ●; all other samples, ○. "Ages" of reservoir backwaters refer to time elapsed since onset of impoundment.

TABLE 11. Average chlorophyll-*a* content of water in northwest sector (main-stem region) of Notigi Reservoir for days 154–267 of the years 1973–76. The 1973 value was recorded prior to the time (t_o) when impoundment was commenced.

Year	Chlorophyll-*a* (μg/L)
1973	5.4
- - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - t_o
1974	8.1
1975	12
1976	13

which evidently represents the norm for the surface waters of the field area.

Among the three reservoir backwaters, the quantity of P or N per unit weight of total dissolved solids decrease in the order Notigi > Kettle > Kelsey (i·e. younger > older) (Fig. 8B–D), suggesting that in the study area impoundment causes an initial upsurge in the proportions of P and N to other dissolved constituents (probably owing to rapid leaching from flooded land) followed by a progressive decline leading to a return to normal background levels several years after impoundment. The excess nutrients initially released into the water were at least partly available for algal growth, as indicated by data from Notigi Reservoir showing an increase in the mean summer chlorophyll content of the water after the onset of impoundment (Table 11) (also see Campbell et al. 1975; Ostrofsky and Duthie 1978).

On the other hand, the Kettle backwater had a larger quantity of dissolved P per unit volume of water than any other sample, and the proportions of P and N in the backwater to P and N in the associated main-stem water were higher for Kettle Reservoir than for the other three bodies of water (Table 2; Fig. 8A). Moreover, the Kettle backwater had the smallest proportion of ortho-PO_4 to total dissolved P, indicating that the anomalously high P levels are attributable to forms of P other than free ortho-PO_4. In spite of being enriched in dissolved P, the Kettle backwater had a lower level of primary productivity than the other reservoir waters (Table 2), suggesting that it is in the "trophic depression" phase. We initially postulated that this trophic depression had arisen because most of the dissolved P was fixed in biologically unavailable forms such as humic-Fe-phosphate complexes (Hecky and Harper 1974; Jackson and Hecky 1977). Although fixation of P by humic-metal complexes is not ruled out by our data and may well occur in the lake and reservoir waters (Fig. 5, 8B–C), the evidence presented in this report favors the interpretation that the available forms of P in the Kettle backwater were not being fully utilized by the phytoplankton owing to a deficiency in trace metals (e.g. Fe) caused by the sequestering of these metals by humic matter.

Another noteworthy observation is that the Kettle backwater had an anomalous Al:Fe ratio with respect to the other water samples. Whereas the other samples gave a highly significant positive correlation between the Al:Fe ratios of the colloidal and total dissolved solids, the Kettle backwater was aberrant because its total Al content, but not its colloidal Al content, was anomalously high (Fig. 9; Table 3). Thus, the Kettle backwater presumably had an abnormally high concentration of low molecular weight (dialyzable) dissolved Al. Considering that Al(III), like Fe(III), has a strong affinity for phosphate (Larsen 1959; Lévesque and Schnitzer 1967; Schnitzer 1969; Sinha 1971), there could be a direct cause-and-effect relationship between the exceptionally high levels of dissolved Al and P in the Kettle backwater.

We have presented a limited set of data suggesting the appearance of temporary perturbations in the geochemistry and productivity of impounded waters within 3 yr following impoundment· Our observations, though based on single water samples, are consistent with physicochemical and primary-production data for multiple paired water samples collected at the backwater and main-stem stations of Kettle Reservoir in different seasons during the period 1972–73 (Cleugh 1974; Hecky and Harper 1974), indicating that our results are not fortuitous (Table 12). According to

TABLE 12. Physical, chemical, and biological-production data for paired water samples collected from the backwater and main-stem stations of Kettle Reservoir during the period 1972–74. Data for 1972–73 were taken from Cleugh (1974) and Hecky and Harper (1974). ("n.d." means no data.)

Station	Date(s)	No. of observations	Chlorophyll-*a* (mg/m³)	TDP	TDN	DOC (μmol/L)	Fe	P/org. C	Color (Pt units)	pH	Primary productivity (mgC·m⁻³·h⁻¹)	*k*	α	Secchi disc(m)
Backwater	June–Oct. 1972	5	2.3	2.1	38.6	90.76	0.0034	0.023	n.d.	7.6	n.d.	n.d.	n.d.	1.8
	March 1973	1	1.0	1.9	29.7	87.01	0.0079	0.022	50	7.3	n.d.	n.d.	n.d.	n.d.
	June–Oct. 1973	4	3.2	2.4	39.3	80.5	0.0032	0.030	n.d.	7.6	n.d.	n.d.	n.d.	2.2
	Sept. 1973	1	3.0	2.7	45.6	100.0	0.0056	0.027	n.d.	7.7	5.0	1.80	n.d.	1.8
	Sept. 1974	1	6.0	5.10	42.8	n.d.	0.001	—	n.d.	7.5	8.6	1.05	2.0	2.1
Main stem	June–Oct. 1972	5	6.0	0.74	28.3	58.2	0.0029	0.013	n.d.	8.2	n.d.	n.d.	n.d.	0.5
	March 1973	1	3.1	0.90	24.1	74.8	0.0020	0.012	15	7.9	n.d.	n.d.	n.d.	n.d.
	June–Oct. 1973	4	2.4	0.58	24.0	48.0	0.001	0.012	n.d.	8.3	n.d.	n.d.	n.d.	0.8
	Sept. 1973	1	2.7	0.58	23.1	69.5	0.0030	0.0083	n.d.	8.4	12	1.3	n.d.	0.8
	Sept. 1974	1	6.7	1.3	27.8	n.d.	0.002	—	n.d.	8.1	15	0.96	6.9	0.8

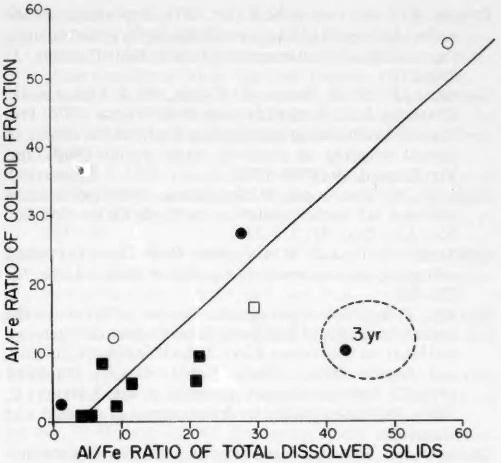

FIG. 9. Relationship between aluminum:iron ratio of colloidal fraction of dissolved solids and aluminum:iron ratio of total dissolved solids (for all samples except the 3-yr reservoir backwater, $r = 0.928$; $P < 0.001$). Explanation of symbols — reservoirs: backwater, ●; main stem, ○; Southern Indian Lake: backwater, ■; main stem, □.

these data, concentrations of dissolved P and N were much higher in the backwater region than in the main-stem region, but primary productivity was much lower, and algal standing crops (as measured by chlorophyll concentration) were either less abundant or virtually the same (within experimental and sampling error). The backwater zone had considerably higher concentrations of dissolved org. C, more intense coloration, a generally higher Fe content, a higher P:org. C ratio, and lower pH values. These observations are at least consistent with the hypothesis that the backwater region was enriched in humic substances which depressed algal productivity. The differences in productivity between the backwater and main-stem stations cannot be attributed to differences in physical factors such as thermal stratification, depth of water, and light penetration. No significant thermal stratification was detected at either station, and light penetration was similar at both stations (or more favorable at the backwater station). Furthermore, the water was shallower at the backwater site (7–8 m) than at the main-stem site (16–22 m); on the basis of critical depth alone (Sverdrup 1953), productivity should have been higher at the backwater station, whereas the reverse was true.

Among the water samples as a whole, not including the aberrant ones from the Notigi and Kettle backwater stations, dissolved P was more strongly correlated with A_{465nm} than with any other chemical parameter. Thus, the degree of association between total P and total Fe, Al, org. C, and A_{465nm} decreased in the order A_{465nm} > Fe > org. C > Al (Table 13). We tentatively infer that most of the dissolved P in the surface waters of the field area is normally in the form of humic-iron-phosphate complexes. The Sephadex elution patterns (Fig. 5) support this interpretation. Similarly, most of the dissolved N is probably in the form of organic compounds. On the other hand, the excess P and N released into the younger reservoir backwaters following impoundment are probably not in the same form as the P and N of the "normal" surface waters, as suggested by the abnormally high concentrations of P and N relative to other chemical parameters (Fig. 8). Dialysis obliterated the distinction between "normal" waters and "abnormal" (Notigi and Kettle) waters (Table 3), suggesting that the excess P and N initially released into the impounded backwaters had relatively low molecular weights. This may account for their apparent availability to phytoplankton (Table 11).

According to our interpretation, impoundment initially causes rapid leaching of available nutrients, including P and N, from inundated soil and vegetation, thereby stimulating an upsurge in primary production

TABLE 13. Correlation matrix relating total dissolved phosphorus to total dissolved iron, aluminum, organic carbon, and "humic matter" (represented by absorption of light at 465 nm) in the water samples, excluding those from the Notigi and Kettle backwater stations. "n.s." means not significant.[a] The analytical data employed represent concentration in the water (on a volume basis) as well as concentration in the freeze-dried dissolved solids (on a weight basis).

		A_{465nm}		Fe		org. C		Al	
		r	P	r	P	r	P	r	P
P	Based on composition of water	0.941	<0.001	0.878	<0.001	0.863	<0.001	0.838	<0.01; >0.001
	Based on composition of dissolved solids	0.867	<0.001	0.833	<0.01; >0.001	0.435	n.s.	−0.104	n.s.

[a] The P-value of each "insignificant" correlation in this table is >0.1. Numerical P-values are given only if they are "significant."

and algal biomass. Humic substances released more slowly into the water subsequently bring about a progressive decline in productivity by sequestering Fe and other trace metals, thus preventing the algae from taking full advantage of the available P and N. This interpretation is consistent with the observation that Kettle Reservoir displayed an anomalously low level of productivity despite the presence of supposedly available low molecular weight forms of P leached from flooded land. Toxic effects of other dissolved organics and the binding of phosphate by humic complexes of Fe and Al could conceivably contribute to the ensuing environmental deterioration. Accumulation of humic matter in the water is made possible by the fact that humic substances are generally very resistant to biodegradation. The "trophic depression phase" is inaugurated when the adverse effect of the humic matter exceeds the beneficial effect of the available nutrients. The trophic depression phase probably comes to an end when the "pulse" of foreign humic matter is dissipated by processes such as sedimentation and flushing. But even under natural, unperturbed conditions, the productivity of surface waters in the field area is limited to a greater or lesser extent by dispersed humic matter.

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Accumulation of Benzo[*a*]pyrene in a Larval Bivalve via Trophic Transfer

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DOBROSKI, C. J., JR., AND C. E. EPIFANIO. 1980. Accumulation of benzo[*a*]pyrene in a larval bivalve via trophic transfer. Can. J. Fish. Aquat. Sci. 37: 2318–2322.

The diatom *Thalassiosira pseudonana* was cultured in 10 μg/L ^{14}C-benzo[*a*]pyrene (B[*a*]P) and subsequently fed to larvae of the hard clam *Mercenaria mercenaria*. The rate of direct uptake of B[*a*]P from seawater by the diatoms was much greater than the rate of trophic transfer of B[*a*]P from the diatoms to the clam larvae. This was attributed to greater efficiency of direct uptake and to the larger quantity of B[*a*]P available in the water. A comparison of direct uptake by bivalves (as reported in the literature) with trophic transfer measured in the present investigation indicated that the processes may be equally important in accumulation of B[*a*]P in natural populations of bivalves.

Key words: benzo[*a*]pyrene, trophic transfer, bivalve larvae

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La diatomée *Thalassiosira pseudonana* a été cultivée dans 10 μg/L de ^{14}C-benzo[*a*]pyrène (B[*a*]P) et ensuite donnée en nourriture à des larves de praire américaine *Mercenaria mercenaria*. Le taux de captation directe de B[*a*]P de l'eau de mer par les diatomées est de beaucoup supérieur au taux de transfert trophique de B[*a*]P des diatomées aux larves de praire. On attribue ce phénomène à une plus grande efficacité de captation directe et à une plus forte quantité de B[*a*]P disponible dans l'eau. Une comparaison de la captation directe par les bivalves (telle que décrite dans les travaux publiés) avec le transfert trophique mesuré au cours de la présente investigation indique que les processus peuvent être également importants dans l'accumulation de B[*a*]P chez des populations naturelles de bivalves.

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OF the various petroleum pollutants found in marine environments, polycyclic aromatic hydrocarbons are among the more insidious, due mainly to their mutagenic and suspected carcinogenic properties (Blumer 1976). One such compound, benzo[*a*]pyrene, has been detected in sediments from widely separated marine and aquatic environments and in the tissues of a diversity of marine organisms (National Academy of Sciences 1975). Accumulation of this compound in the marine biota of various geographical locations has been correlated with the level of pollution from industrial sources (Neff et al. 1976), but the mode of uptake is not clear.

There is considerable evidence that polycyclic aromatic compounds are accumulated directly from seawater by many organisms (for a review, see Lee 1977); however, transfer through the food chain has been less convincingly documented. In fact, Korte and Boedefeld (1978) concluded that no important accumulation of any petroleum hydrocarbon occurs through ingestion of contaminated food and that consequently no food-web magnification of petroleum hydrocarbons occurs. But, this seems rather unlikely in light of the well-documented trophic magnification of other lipid-soluble compounds such as chlorinated hydrocarbons (e.g. Risebrough et al. 1967; Woodwell et al. 1967; DeLong et al. 1973) and additional study of the problem appears necessary.

In the present paper, we report results of an investigation of the uptake of benzo[*a*]pyrene (B[*a*]P) by a diatom and the transfer of this material to a larval bivalve fed a diet consisting solely of this diatom.

Materials and Methods

The diatom *Thalassiosira pseudonana* 3H Hasle and Heimdal (Hustedt) was cultured in a medium containing ^{14}C-bezo[*a*]pyrene and subsequently fed to larvae of the hard clam *Mercenaria mercenaria*. Accumulation of B[*a*]P by the diatoms and trophic transfer to the larval clams were measured by liquid scintillation spectrometry. It is possible that some decomposition of the B[*a*]P occurred during the experiment due to bacterial metabolism and photodegradation (Suess 1976) and some of the radioactivity accumulated by the organisms was undoubtedly due to degradation products.

^{14}C-B[*a*]P was purchased from Amersham–Searle Corporation and had a specific activity of 7.44 MBq/mg. The material was supplied in a benzene solution in a glass ampoule sealed under nitrogen to prevent oxidation.

Radioassays throughout the experiment were performed

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with a Beckman LS-100 Liquid Scintillation System using a fixed-window isoset with a wide-range window for ^{14}C. Corrections were always made for counting efficiency (as determined with a ^{14}C-toluene standard) and background. Quench corrections were made using the external standard ratio method. All samples were counted in 20-mL liquid scintillation vials to which 9 mL of scintillation counting fluid (6 g PPO, 500 mL Triton X-100, and 500 mL toluene/L) were added.

As B[*a*]P is nearly insoluble in seawater, it was necessary first to dissolve the compound in a nontoxic carrier solvent, polyethylene glycol (Carbowax 4000); this solvent had been used successfully in an earlier study with the cyclodiene pesticide, dieldrin (Epifanio 1971). ^{14}C-B[*a*]P was recovered from its original benzene solution by passing a stream of nitrogen over the surface while the solution was warmed to 50°C in a water bath. The residual material was then dissolved in 10 mL of polyethylene glycol. The actual concentration of ^{14}C-B[*a*]P in the stock solution was determined by radioassay of eight aliquots of a 500:1 dilution of the stock. That analysis indicated a concentration of 2.51 ± 0.03 mg/L in the stock solution.

^{14}C-B[*a*]P was dissolved in seawater by pipetting stock solution beneath the surface and stirring for 1 min. The accuracy of the dilution technique was checked by addition of 0.1 mL of stock solution to each of three 1-L flasks filled with 250 mL of seawater, giving a nominal concentration of 10 µg/L. The seawater was then analyzed for ^{14}C-B[*a*]P by shaking a 20-mL aliquot for 1 min in a 125-mL separatory funnel with 20 mL of liquid scintillation counting fluid (Epifanio 1973). The water was removed and subsequent radioassay of the counting fluid allowed a calculation of 9.26 ± 0.53 µg/L in the seawater.

ALGAL CULTURE

Unialgal cultures of *Thalassiosira pseudonana* were cultured at 20°C, 30‰ salinity under cool-white fluorescent light (Westinghouse Corporation) in modified *f/2* medium (Guillard and Ryther 1962). The concentration of algae in suspension was monitored with a Coulter Counter Model Z_B fitted with a 70-µm aperture.

An initial experiment was conducted to determine the variability in uptake of ^{14}C-B[*a*]P by algae from different cultures. This was important because it was necessary to use algae from a different culture each day when feeding the larval bivalves. This initial experiment involved six different cultures. To test a particular algal culture, diatoms were first grown in a 19-L carboy inoculated at 5.0×10^4 cells/mL. When the concentration in the carboy reached approximately 3.5×10^6 cells/mL, an aliquot of algal suspension was removed and split evenly into five, 2-L Erlenmeyer flasks. A quantity of sterile culture medium was then added to each flask until the volume was 1 L and the density of algal suspension was 2.5×10^6 cells/mL. Four of the flasks were inoculated with 0.4 mL of ^{14}C-B[*a*]P stock solution yielding nominal concentrations of 10 µg/L B[*a*]P. Following a 24-h incubation under fluorescent light and aeration, triplicate Coulter Counter determinations were made of the number of algal cells in the culture containing no ^{14}C-B[*a*]P. This value was assumed to be similar to the density of suspension in each of the remaining four flasks (a preliminary experiment indicated that 10 µg/L B[*a*]P did not affect algal growth rate).

Seven 50-mL samples were pipetted from each of the four B[*a*]P contaminated cultures and filtered through Whatman GFC glass fiber filters to remove algal cells. Four of these filters were placed in scintillation vials for later radioassay. (To account for possible B[*a*]P adsorption on the filters, five 50 mL volumes of 10 µg/L ^{14}C-B[*a*]P in seawater were also filtered and radio-assayed. Adsorption was slight but was considered part of background and subtracted from experimental values.) The three remaining filters (pretared) were used to determine dry weight of the algal cells. They were rinsed in 50 mL of 0.5 mol/L ammonium formate to remove sea salts, dried at 85°C to volatilize ammonium formate, and weighed on an analytical balance.

Because the feeding experiment with larval hard clams involved daily centrifuging of B[*a*]P-contaminated algae from suspension with later resuspension in uncontaminated water, we were also interested in the effect of centrifuging on the concentration of B[*a*]P in the algae and the possibility of excretion of B[*a*]P into uncontaminated water by the algae. To obtain baseline information on these phenomena, the remaining algae from each of the four B[*a*]P-contaminated flasks were centrifuged from suspension at 4°C, 10 000 rpm using a DuPont Sorval RC-5 refrigerated centrifuge. Following centrifugation, the diatoms were resuspended in five flasks of filtered seawater (20°C, 30‰ salinity) and six 50-mL samples were pipetted from each flask for radioassay. The remaining algae in each flask were incubated for 24 h (20°C) to determine loss of B[*a*]P to the seawater. After this 24-h period, six 50-mL aliquots were taken from each flask for radioassay.

HARD CLAM LARVAE AND THE FEEDING EXPERIMENT

Larvae used in the experiment were the progeny of wild clams collected locally. Spawning was induced by temperature shock and addition of sperm from the gonads of ripe males (Loosanoff and Davis 1963). Eggs from three females were exposed to sperm from three males, and the resultant embryos mixed together to ensure genetic heterogeneity of the experimental larvae. Following a 36-h developmental period, 50 000 larvae were placed in each of ten, 15-L plastic rearing vessels containing 10 L of filtered seawater (25°C, 30‰ salinity) for subsequent use in the larval feeding experiment.

Since algae in different physiological states may take up B[*a*]P at different rates, it was important that all algae used in the feeding experiment were from a similar stage of culture. We inoculated one 19-L carboy each day beginning 4 d before initiation of the feeding experiment. For example, on Day -4 one 19-L carboy was inoculated at 5.0×10^4 cells/mL and by Day -1 the density of algal suspension in the carboy had reached approximately 3.5×10^6 cells/mL. A portion of this culture was then divided equally among five 2-L Erlenmeyer flasks (four containing ^{14}C-B[*a*]P-contaminated medium and one containing uncontaminated medium). The amount of algae added to each flask was such that the density of suspension was 2.5×10^6 cells/mL when the volume was adjusted to 1 L. The nominal concentration of the ^{14}C-B[*a*]P in the contaminated flasks was 10 µg/L. Each flask was then incubated for 24 h at 20°C under fluorescent light and the algae then used as food for the larval hard clams (Day 1). Similarly, algae originally from a carboy inoculated on Day -3 were fed to the larvae on Day 2, algae from a carboy inoculated on Day -2 were fed on Day 3 and so forth until Day 9. The density of algal suspension in the control culture was determined daily with a Coulter Counter Model Z_B (it was generally near 3.5×10^6 cells/mL) and was assumed to be the same as densities in contaminated cultures on that day. Algae from both control and contaminated cultures were then centrifuged from suspension and subsequently dispersed in uncontaminated seawater before being fed to the larvae. Daily initial concentration of algae in each rearing container was 1×10^5 cells/mL; this always represented an excess of food.

Day 1 commenced after a 36-h period of pre-veliger development, and water in each rearing vessel was changed daily during the following 9 d by siphoning through a stainless steel seive (37 μm openings) upon which larvae were collected. (All algal cells passed through the seive). Larvae in nine of the rearing containers were fed ^{14}C-B[*a*]P-contaminated algae while those in the remaining rearing vessel were fed uncontaminated algae. Each day larvae from the nine vessels receiving contaminated food were mixed together in a common container containing 9-L filtered seawater; 1 L of this larval mixture was taken daily for subsequent radioassay and the remainder redistributed to the nine rearing vessels.

The 1-L radioassay sample was further divided into two 500-mL portions. One portion was partitioned into ten 50-mL aliquots, and each aliquot filtered through a Whatman GFC glass fiber filter. After a rinse with 20-mL clean seawater, seven filters were placed in scintillation vials containing 2-mL Soluene (New England Nuclear) to dissolve soft tissue. After several hours, 10-mL scintillation counting fluid were added and the radioassay conducted as described above. To estimate the daily dry weight of the larvae, we rinsed the three remaining pre-tared filters in 0.5 mol/L ammonium formate, dried for 24 h at 85°C, and weighed on an analytical balance. A 500-mL sample from the rearing vessel receiving uncontaminated algae was subjected to identical radioassay procedures

Depuration of ^{14}C-B[*a*]P was estimated daily by placing the second 500-mL portion of the radioassay sample in a rearing vessel containing 5 L of filtered seawater and feeding uncontaminated algae for 24 h. Larvae were then concentrated in 500-mL filtered seawater and a 250-mL sample (in ten 25-mL aliquots) was subjected to radioassay and dry weight analysis as above. The remaining 250 mL were placed in a rearing vessel containing 2.5 L of filtered seawater and fed uncontaminated algae for an additional 24 h, giving these larvae a total depuration period of 48 h. Radioassay was then conducted on these larvae as well.

Results

ACCUMULATION OF ^{14}C-BENZO[*a*]PYRENE BY DIATOMS

There was no significant difference (ANOVA: $P \leq 0.05$) in the 24-h accumulation of ^{14}C-B[*a*]P by diatoms from six different cultures tested on six different days (Table 1). Furthermore, a comparison (*t*-test: $P \leq 0.05$) of initial measurements of accumulation with corresponding measurements after algae had been centrifuged and resuspended, showed a significant difference in only one case. This loss of B[*a*]P was probably due to lysis of some of the cells during centrifugation but it is not clear why it occurred in only one culture. However, a comparison (*t*-test) of B[*a*]P residues immediately after centrifugation with those after 24-h depuration in uncontaminated seawater never showed significant differences between corresponding measurements. Thus it was concluded that while there may be some loss of B[*a*]P during centrifugation, there is no significant loss of B[*a*]P from resuspended algae over at least a 24-h period and that consequently, uptake of B[*a*]P by hard clam larvae was totally a function of ingestion of contaminated food.

TABLE 1. Comparison of mean concentration of ^{14}C-benzo[*a*]-pyrene in *Thalassiosira pseudonana* after 24-h incubation, centrifugation and resuspension, and 24-h depuration. Each day represents a different culture. Values are μg benzo[*a*]pyrene per g (dry weight) of diatom. NM = not measured.

	Culture					
Condition	1	2	3	4	5	6
Incubation	40.5	42.8	40.4	39.3	46.7	43.2
Centrifugation and resuspension	NM	NM	37.8	38.9	40.4	40.4
Depuration	37.3	42.7	35.8	37.8	37.0	38.7

ACCUMULATION OF ^{14}C-BENZO[*a*]PYRENE BY HARD CLAM LARVAE

Two separate runs of this experiment were conducted and the results were pooled. Clearly, the rate of accumulation of ^{14}C-B[*a*]P by hard clam larvae is described by a straight line as generated from least-squares regression analysis (Fig. 1). However, larvae that had accumulated B[*a*]P via contaminated food were able to rid themselves of considerable quantities of the compound when placed in filtered seawater and fed uncontaminated diatoms for 24 h. Depuration over the first 8 d was a constant percentage (approximately 44%) of the originally accumulated B[*a*]P and least-squares regression showed high correlation between B[*a*]P residue after depuration and time of exposure to contaminated food. Larvae that began depuration on Day 9 were relatively unsuccessful in ridding themselves of B[*a*]P. This was apparently related to the onset of metamorphosis in the larvae.

The amount of depuration effected by an additional 24 h with uncontaminated food was less than in the first 24 h but there was again a high correlation between final B[*a*]P residue and total time of exposure to contaminated food. As with the 24-h depuration, Day 9 larvae were less able to expurge B[*a*]P from their tissues.

Discussion

Results of our study have corroborated earlier investigations showing direct uptake of aromatic hydrocarbons by phytoplanktors (Lee 1977), but more importantly, we have documented significant trophic transfer of benzo[*a*]pyrene to a herbivore. The diatom *Thalassiosira pseudonana*, when exposed to a 10 μg/L solution of B[*a*]P for 24 h, accumulated a mean tissue level of 42.2 μg/g while *Mercenaria mercenaria* larvae fed these diatoms accumulated 18.6 μg/g after 9 d.

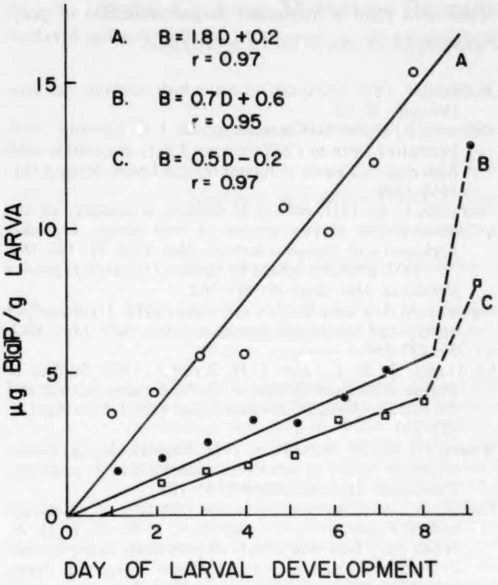

FIG. 1. Accumulation and depuration of B[*a*]P by larvae of the clam *Mercenaria mercenaria*. A, Accumulation of ^{14}C-benzo[*a*]pyrene by larvae fed contaminated algae; B, Retention of ^{14}C-benzo[*a*]pyrene by larvae after 24-h depuration; C, Retention of ^{14}C-benzo[*a*]pyrene by larvae after 48-h depuration.

So the rate of direct uptake by the algae, was approximately 20 times faster than the rate of trophic transfer. As can be seen in the following calculations, this was partially due to the fact that there was nearly 6 times as much B[*a*]P available for uptake per gram of alga per day than available for trophic transfer per gram of larva per day (Equation [3] ÷ Equation [9]) and partially due to the fact that efficiency of uptake was almost 4 times greater than efficiency of trophic transfer (Equation [4] ÷ Equation [10]).

In the case of the diatoms accumulating B[*a*]P directly from seawater, efficiency can be calculated as:

(1) Total B[*a*]P in solution in algal culture:
$(1 \times 10^{-8}$ g-B[*a*]P/g water$) \times (1 \times 10^{3}$ g water/culture$) = 1.0 \times 10^{-5}$ g-B[*a*]P/culture.

(2) Dry weight of algae per culture[1]:
$(3.5 \times 10^{9}$ cells/culture$) \times (13.2 \times 10^{-12}$ g-algae/cell$) = 4.6 \times 10^{-2}$ g-algae/culture.

(3) Maximum daily accumulation by algae:
$(1.0 \times 10^{-5}$ g-B[*a*]P/culture$) \div (4.6 \times 10^{-2}$ g-algae/culture$) = 2.2 \times 10^{-4}$ g-B[*a*]P/g-algae.

(4) Efficiency of accumulation:
$(4.2 \times 10^{-5}$ g-B[*a*]P accumulated/g-algae$) \div (2.2 \times 10^{-4}$ g-B[*a*]P available/g-algae$) \times 100 = 19.1\%$.

Maximum possible accumulation by hard clam larvae can be estimated by assuming a 10% gross growth efficiency over the period of larval development:

(5) Larval growth (Day 1 through Day 9)[1]:
$(6.0 \times 10^{-7}$ g-larvae/Day 9 larva$) - (1.0 \times 10^{-7}$ g-larvae/Day 1 larva$) = 5.0 \times 10^{-7}$ g-larvae/larva.

(6) Alga consumed with 10% growth efficiency:
$(5.0 \times 10^{-7}$ g-larvae/larva$) \div (1 \times 10^{-1}$ g-larvae/g-algae$) = 5 \times 10^{-6}$ g-algae/larva.

(7) Total B[*a*]P consumed:
$(5.0 \times 10^{-6}$ g-algae/Day 9 larva$) \times (4.2 \times 10^{-5}$ g-B[*a*]P/g-algae$) = 2.1 \times 10^{-10}$ g-B[*a*]P/Day 9 larva.

(8) Maximum accumulation over 9 d:
$(2.1 \times 10^{-10}$ g-B[*a*]P/Day 9 larva$) \div (6.0 \times 10^{-7}$ g-larvae/Day 9 larva$) = 3.5 \times 10^{-4}$ g-B[*a*]P/g-larva.

(9) Maximum daily accumulation:
$(3.5 \times 10^{-4}$ g-B[*a*]P/g-larva$) \div 9$ d $= 3.8 \times 10^{-5}$ g-B[*a*]P/g-larva·d^{-1}.

(10) Efficiency of accumulation:

$$\frac{(1.9 \times 10^{-5} \text{ g B}[a]\text{P transferred/g-larva})}{(3.5 \times 10^{-4} \text{ g-B}[a]\text{P/g-larva})} \times 100 = 5.4\%$$

The higher efficiency of uptake of B[*a*]P from seawater is interesting in light of the fact that the concentration of this compound in the larval food was more than 1800 times greater than that in the seawater of the algal culture medium. The dilute solution in water was apparently compensated by the high partition coefficient concerning B[*a*]P dissolved in water and in the algal lipids and further compensated by continuous stirring of the algal cultures. In contrast, the partition coefficient concerning B[*a*]P in the food and that in larval tissue was undoubtedly low (since both contain considerable lipid) and uptake may have been associated with efficiency of digestion and assimilation of the algae. Any algal lipid egested by the larvae would carry its B[*a*]P with it and this B[*a*]P would not be available for uptake. Also, any B[*a*]P adsorbed to the undigestible cell casings (frustrules) of the diatoms would be lost to egestion. We did not attempt to ascertain the relative amount of algal B[*a*]P attributable to adsorption, but it was probably significant due to the siliceous composition of the frustrules and high surface-to-volume ratios of the algal cells. High adsorption would not only contribute to low efficiency of trophic transfer, but would also increase the apparent efficiency of direct uptake from seawater.

In the present work the rate of trophic transfer remained linear throughout larval development. Presumably, accumulation would continue postmetamorphosis (although not necessarily at the same rate) until the storage compartments of the clams became saturated with B[*a*]P; Stegeman and Teal (1973) found that petroleum hydrocarbons accumulated to more than 300 μg/g in the soft tissues of oysters before saturation occurred. This, however, is unlikely in all but the most chronically polluted environments as depuration of hydrocarbons occurs rapidly in the absence of renewed input. Earlier work has shown that most B[*a*]P is purged from bivalves during the 1st wk of depuration and that only a small residual remains for an additional 4–8 wk (Lee et al. 1972; Neff et al. 1976; Stegeman and Teal 1973). In our study, rapid, but less than total, depuration was observed over 2 d. Release of B[*a*]P was proportional to the amount accumulated in the tissues; 56% of the amount accumulated through a given day of larval development was expelled after 24-h depuration and 71% after 48 h. However, the amount of depuration of B[*a*]P in Day 9 larvae was much less than that on previous days. Many of the larvae began to metamorphosis on Day 9, but it is not clear why this should have affected depuration.

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[1] Values for algal weights and larval growth were determined during the feeding experiment. See Methods for details.

We know of no other reports of trophic transfer of B[*a*]P to bivalve molluscs, but there have been investigations of direct uptake. For example, Neff and Anderson (1975) exposed *Rangia cuneata* to 30 μg/L B[*a*]P and reported an accumulation of 6.2 $\mu g/g \cdot d^{-1}$. Results of experiments with other aromatic hydrocarbons have shown similar rates of uptake (Fossato and Canzonier 1976; Stegeman and Teal 1973). Trophic transfer in our investigation was 2.1 $\mu g/g \cdot d^{-1}$ from a food contaminated with 42.2 μg/g B[*a*]P. Assuming that accumulation is proportional to the amount of B[*a*]P in the food, the hypothetical rate of uptake if algae had been contaminated with 30 ng/g B[*a*]P would have been 1.5 $ng/g \cdot d^{-1}$, a rate more than three orders of magnitude less than the direct uptake found by Neff and Anderson. So, in a situation where the concentration of B[*a*]P in water and in food is similar, direct uptake from water is much greater. Roesijadi et al. (1978) reported a similar result when comparing the accumulation of B[*a*]P from water and sediment by the clam *Macoma inquinata*.

Nevertheless, under natural conditions the concentration of B[*a*]P in the food of bivalves is likely to be much higher than that in the surrounding water and rates of accumulation of the material from water and food may be similar. For example, in our experiment algae that were cultured in 10 μg/L B[*a*]P concentrated the compound more than three orders of magnitude in 24 h. Clam larvae eating these algal cells accumulated B[*a*]P at approximately 2 $\mu g/g \cdot d^{-1}$. *Rangia cuneata* exposed 30 μg/L in seawater showed a daily accumulation of 6 mg/g B[*a*]P (Neff and Anderson 1975) and if we assume a linear relationship between accumulation and concentration in the water, *Rangia cuneata* would accumulate 2 μg/g B[*a*]P$\cdot d^{-1}$ from 10 μg/L in seawater. This strongly suggests that uptake from both water and food is important in accumulation of polycyclic aromatic hydrocarbons by filter-feeding bivalves.

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Stable Cycles in Multistage Recruitment Models: An Application to the Northern California Dungeness Crab (*Cancer magister*) Fishery

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This study illustrates, through the modeling of the Northern California Dungeness crab fishery, a diagnostic approach to the inference of multistage density-dependent recruitment mechanisms operating in animal populations. Northern California Dungeness crab landings have exhibited a strikingly regular cycling pattern since the early 1940s, but with increasing amplitude swings as the fishery has expanded suggesting the possibility of an eventual crash. A variety of mechanisms have been proposed, involving either biological feedback controls or exogeneous environmental effects, to account for the regular cycling and its possible destabilization by fishing. This study examines the plausibility of various alternative biological control mechanisms by incorporating them, one by one, into a multistage dynamic recruitment model, of nonlinear renewal type, based on general qualitative features of the crustacean's life history. A total of 48 plausible model variants are examined, reflecting differences in intensity and timing of possible feedback controls and uncertainty about exploitation and survival rates.

Model analysis incorporates two complementary approaches to test out the range of alternative hypotheses incorporated in these variants. The first approach is based on examination of qualitative features of model dynamics: period and amplitude of stable cycles, and the model's response to varying levels of exploitation. The second is based upon extracted estimates of probable historic year-class strength and assesses the fit of model variants by least-squares regression techniques. These twin diagnostic procedures allow elimination of most model variants, and support the hypothesis that recruitment must be determined in the very early life stages, egg, or larval.

The last phase of analysis is to further probe the model by numerical experimentation, including a simulation of the institution of female harvest. Finally, the implications of the modeling exercise are drawn, for future field studies and for second generation modeling

Key words: bifurcations, Dungeness crab, *Cancer magister*, stable cycles, multistage recruitment models, stock-recruitment

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La présente étude illustre, à l'aide d'une modélisation de la pêcherie de dormeurs du Pacifique de la Californie septentrionale, une approche diagnostique des effets de mécanismes polyétagés de recrutement dépendants de la densité qui agissent sur les populations animales. Depuis le début des années 1940, les débarquements de dormeurs du Pacifique de la Californie septentrionale sont caractérisés par un cycle remarquablement régulier, mais avec fluctuations dont l'amplitude s'accrût à mesure la pêche se développa, ce qui laisse entrevoir la possibilité d'un affaissement éventuel. Divers mécanismes ont été mis de l'avant, impliquant soit des contrôles de rétroaction biologiques, soit des effets environnementaux exogènes, pour expliquer ces cycles réguliers et leur déstabilisation possible par suite de la pêche. On examine la vraisemblance de divers mécanismes de contrôle biologique en les incorporant, un par un, dans un modèle de recrutement dynamique polyétagé, de type à renouvellement non linéaire, fondé sur les caractéristiques qualitatives générales du cycle biologique du crustacé. Au total, 48 variantes plausibles du modèle ont été examinées, reflétant les différences d'intensité et de chronométrage des contrôles de rétroaction possibles et l'incertitude quant aux taux d'exploitation et de survie.

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L'analyse des modèles incorpore deux approches complémentaires de la vérification de la gamme d'hypothèses comprises dans ces variantes. La première approche est fondée sur l'examen des caractéristiques de la dynamique du modèle : période et amplitude des cycles stables et réactions du modèle à divers niveaux d'exploitation. La deuxième approche repose sur des estimations de l'abondance passée probable des classes d'âge et évalue l'adaptation des variantes du modèle à l'aide de techniques de régressions par moindres carrés. Ces deux méthodes diagnostiques permettent d'éliminer la plupart des variantes du modèle et confirment l'hypothèse que le recrutement doit être déterminé au tout début du cycle biologique, au stade d'oeuf ou de larve.

Dans sa dernière phase, l'analyse explore davantage le modèle par une expérimentation numérique, y compris une simulation d'une récolte des femelles. Enfin, on tire les conclusions de cette modélisation, en vue d'études futures sur le terrain et de modèles de seconde génération.

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DESCRIPTION of the mechanisms underlying variable year-class strength at recruitment has been characterized as the most critical problem in fish population dynamics (Paulik 1973; Gulland 1974; Cushing 1973b). Indeed, biological control mechanisms which stabilize populations in single species models invariably are assumed to involve nonlinear feedback through which adult population numbers influence either natality or prerecruitment survival (Paulik 1973). The celebrated models of Ricker (1954) and Beverton-Holt (1957) describe the feedback process through a first order difference equation of the form

$$R(t + \tau) = G[S(t)],$$

where $R(t + \tau)$ is recruitment at some lag interval τ from the spawning of adult fish $S(t)$ at time t. Though simple, this model is already capable of capturing the effects of nonlinear density-dependence in establishing stable population levels or, in some cases, leading to persistent cycling of population size. Although the above form of model is restricted to single-age spawning classes, replacing S by a weighted average $S_b = m_1S_1(t) + \ldots + m_kS_k(t)$ of adult age-class numbers allows modeling of repeated spawning in an age-structured adult population. However, such an improved model still assumes that the feedback control is exerted in a single time interval, that is, at a single stage (usually egg or larval) in the life history of the young cohort.

Recruitment in many fish populations may not be so simply determined. In particular, both natality and juvenile survival may independently involve feedback influences. Competition with or cannibalism by older juveniles upon incoming year-classes may have significant impact on resulting year-class strength. Adult centrarchids, such as the largemouth bass, *Micropterus salmoides*, are commonly in association with their fry during a short period of time when density-dependent adult-related mortality might occur. Yearling bass, produced by the adult stock a year previous, inhabit shallow water areas and may prey extensively upon young-of-the-year bass, thus creating a more complex recruitment process (Ricker 1954). Hankin (1978, 1980) found that recruitment of new individuals to laboratory guppy (*Poecilia reticulata*) populations was determined by both adult and juvenile population components. To survive, newly born fry had to successfully elude adult predators outside a refuge area, and also avoid juvenile predators (or competitors) within the refuge.

Density-dependent mortality may also occur when recruited fish first enter the adult population, at time t_r in the notation of Beverton and Holt (1957). This seems especially possible for crustaceans, such as the Dungeness crab (*Cancer magister*), where large adults may cannibalize smaller juveniles but where adults and larval stages are not in contact (MacKay 1942; Gotschall 1977). These more complex mechanisms create recruitment relations which we shall refer to as multistage recruitment processes. These concepts have been discussed by Larkin et al. (1964) and Paulik (1973).

The literature does not abound with documented examples of such complex multistage recruitment mechanisms, probably because of statistical difficulties in discovering such processes. Typical plots of presumably simple, standard stock-recruitment relations are usually disappointingly without trend and one must be rather arrogant to force a curve through such scatter (e.g. Cushing 1973a). Moreover, as Paulik (1973) pointed out, with multistage processes "quite different component processes may generate superficially similar reproductive curves." If, in fact, a more complex process were operative, say when recruitment depended in different ways on adult densities at two times previous, one would have the statistical problem of elucidating a function which may be nonlinear in two variables, based on collection of (usually) single data points per year (Hankin 1978).

The fishery biologist may likely never collect enough data to allow confident statistical descriptions of such complex processes. However, enough general biological knowledge may be available — and this is the principle thesis of the present paper — to allow incorporating plausible alternative hypotheses into variants of a basic model and, by analyzing the contrasting qualitative behavior of these variants, to discard certain mechanisms and to single out others for more thorough examination.

The type of model which we investigate in detail may be described as a nonlinear Leslie matrix which, by focusing on a particular life stage, may be recast as a nonlinear renewal equation. Density dependence is expressed through the presence in the model of one or several nonlinear feedback functions, with the shape of each determined by a few (say 2 or 3) undetermined parameters. Mathematical analysis of the model involves a search for qualitative shifts in solution characteristics which may result from adjusting parameter values. Of particular interest is the so-called Hopf bifurcation, where a stable equilibrium goes over to stable cycling. Bifurcations have enjoyed some recent attention in the theoretical ecology literature (Oster and Guckenheimer 1976; MacDonald 1977).

Discrete nonlinear renewal equations have been proposed previously in fisheries biology by Allen and Basasibwaki (1974), who carried out a linear stability analysis for an equation which incorporated a single-time compensatory mechanism (which they interpreted as egg or larval mortality). They also carried out simulation studies.

Much of the present paper is given over to an analysis, by the strategy described above, of mechanisms that have been proposed to explain the observed regular pattern of variations in the annual catch of Dungeness crab in Northern California. This pattern seems to show a regular periodicity, but also increasing amplitude swings, possibly foreshadowing a crash. Peterson (1973) showed a correlation of crab harvests with nutrient upwelling patterns, but then Botsford and Wickham (1975) displayed additional statistical evidence which suggested that the regular cycling might better be explained by some internal population control. In a later paper (1978) they proposed a model, a continuous version of that of Allen and Basasibwaki, and used it to analyze the effect of fishing pressure.

Botsford and Wickham suggested several possible mechanisms for internal density-dependent control of population levels, including cannibalism of juveniles by adults, and maternal-density related egg predation by a nemertean worm. They cited evidence from their model simulations that the increase of fishing pressure could be destabilizing the Northern California crab populations, possibly leading to a (permanent?) population decline like that which occurred in the early 1960s in the Central California fishery.

In this paper we test these and other hypotheses of density-dependent controls of Dungeness crab numbers, with the use of a multistage recruitment model, one tailored to what is known of the life history of *Cancer magister*. In fact we build a whole series of models, incorporating a variety of assumptions about the form, intensity, and phasing of feedback mechanisms. We then carry out a full nonlinear analysis of the models — linear analysis alone being inadequate for investigating stable cycling behavior. The modeled system may be compared with the natural one by either of two methods: The first is to compare model output with historical population time series — in this, waveform, cycle period, and amplitude changes are diagnostic. The second method is to utilize empirical data directly in the model, assuming the essential correctness of the adult phase of the model, and assessing statistically the empirical fit of the model's multistage recruitment mechanism. For the Dungeness crab fishery, despite the paucity of empirical data, these two procedures together are remarkably effective in screening down an initially wide set of alternative hypotheses, and in particular casting serious doubt on mechanisms which involve juvenile mortality or the level of fishing pressure on adult males. The two approaches reinforce each other's evidence and point strongly to the hypothesis that year-class strength is in fact established during egg and larval stages — prior to the settling out of juveniles. This does not rule out the possibility that density dependence and environmental effects might be operating jointly during these early life stages.

Our conclusions can hardly be definitive — the empirical data are far too scanty for that. But the modeling does provide a first step in an iterative modeling process, by pointing out clearly the kind of data that must be gathered before one can hope to resolve present ambiguities. In particular, using the model for simulation of the effect of management manipulations, such as changes in fishing pressure or the institution of female harvesting, suggests experiments which could discriminate between plausible alternative control mechanisms.

Northern California Dungeness Crab (*Cancer magister*) Fishery

The Dungeness crab supports substantial fisheries along the North American Pacific coast. Regulation of fisheries is similar in all areas; only males are harvested and a seasonal closure is used to restrict harvest of soft-shell males. A minimum size limit (160–165 mm carapace width) is enforced for males and allows them to breed at least once before capture, thus ensuring insemination of the protected female reproductive pool (Poole and Gotschall 1965). All Pacific coast fisheries have exhibited large fluctuations in annual harvest and in Northern California, in particular, harvests appear to fluctuate in a cyclic pattern (Fig. 1) with a period of about nine years (Botsford and Wickham 1978).

In Northern California copulation occurs in early summer months, March through August. Eggs are extruded by females in fall (October) and hatch from November through March. The number of eggs laid per female ranges from 700 000 to 2 000 000 and depends on female size (and age). After hatching, Dungeness crab pass through five pelagic larval zooeid stages and a final pelagic megalops stage before metamorphosis and settling approximately one year after copulation of adults.

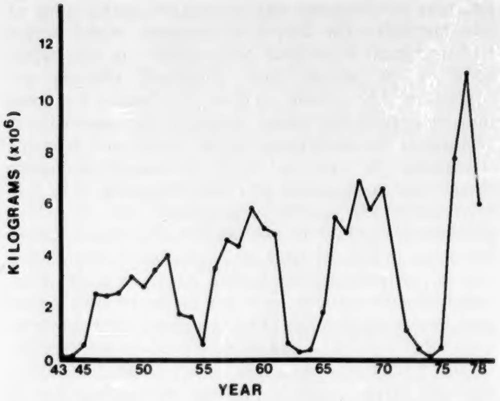


FIG. 1. Annual landings of Dungeness crab in the Northern California fishery, 1943–78.

TABLE 1. Total vessel effort and estimated numbers of pots fished in the Northern California Dungeness crab fishery, 1943–78. Parentheses indicate estimates of total pots used for statistical analyses when pot data were not available.

	Total effort	
Year	Vessels	Pots (×10³)
1943	39	1.23
1944	43	1.98
1945	64	3.33
1946	—	(5.90)
1947	163	8.46
1948	—	(9.29)
1949	—	(10.13)
1950	195	10.96
1951	176	10.13
1952	196	10.98
1953	175	8.98
1954	143	8.71
1955	95	6.31
1956	121	25.50
1957	112	20.93
1958	148	12.08
1959	184	16.82
1960	208	18.91
1961	213	18.11
1962	190	15.56
1963	124	12.01
1964	117	14.11
1965	164	15.26
1966	169	20.28
1967	168	24.63
1968	173	30.90
1969	194	31.32
1970	237	26.39
1971	250	32.03
1972	190	27.54
1973	153	20.96
1974	93	6.10
1975	122	12.73
1976	299	26.00
1977	410	30.75
1978	330	49.50

During the year after settling, the crabs pass through 11 molts and attain maturity about 2 yr after settling at a size of 100–115 mm (Butler 1961; R. Warner, Cal. Dep. Fish and Game, Eureka, CA 95501, personal communication). Once maturity is attained, growth of females is slow relative to males, and females rarely exceed the size of harvestable males (Butler 1960). Slow female growth creates difficulty in aging adult females and, as a result of this difficulty and the prohibition of female harvest, little is known of the age structure of the female reproductive pool. Males attain legal size about 3 yr after settling. Aging of males is performed by length frequency analysis which is accurate until crabs are 4 yr past settling. Beyond this age, overlap in size at age renders the aging technique progressively less reliable. Maximum age for males in the Northern California fishery is believed to be about 6 yr after settling (R. Warner personal communication).

Knowledge of natural mortality, survival, and exploitation rates for adult crab is poor. High recovery rates in limited tagging studies (Cleaver 1949; Jow 1965) indicate that fishing is the predominant source of mortality for males. Jow estimated natural mortality to be about 0.15/yr and Botsford and Wickham (1978) used a 0.2/yr figure in their model of the Dungeness fishery. No published data exist concerning mortality rates of mature females.

Estimates of exploitation rates for harvestable males have ranged from 60 to 98% (PMFC 1977; Gotschall 1978b) and in general it has been assumed that virtually all legal males are captured each season (Cleaver 1949; Peterson 1973; Botsford and Wickham 1978). Annual fluctuations in landings have thus been presumed to roughly reflect annual fluctuations in crab year-class strength or recruitment. Fishing effort, however, measured as total pots, has also fluctuated in a pattern similar to landings and apparently responds to the abundance of harvestable crabs (with perhaps a 1-yr lag). In Northern California recent effort levels have ranged from 6100 pots in 1974 to nearly 50 000 in 1978 (Table 1). With such dramatic fluctuations in effort, it seems quite unlikely that a nearly constant exploitation rate of say 0.85 is in fact achieved.

One normally presumes that broad fluctuations in fishing effort will be reflected by variations in exploitation and survival rates. If significant variations in exploitation rate have occurred, then crab landings are not, without manipulation, an accurate index of year-class strength and the apparent period of landings is not necessarily equivalent to that of year-class strength. Hence it is of interest to examine the implications of a variable exploitation regime.

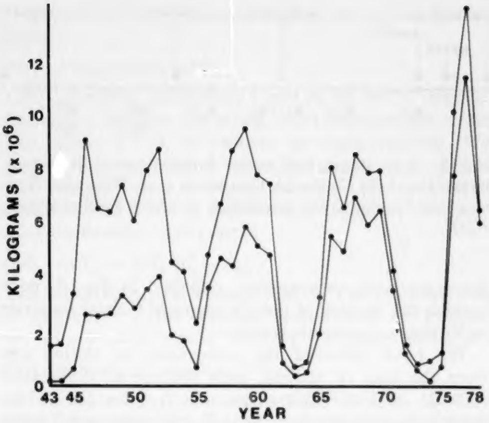


FIG. 2. Annual landings (lower line) and estimated initial harvestable biomass (upper line) of Dungeness crab in the Northern California fishery, 1943–78. Estimated initial abundance assumes $M = 0.22$ and that fishing mortality rate (F) depends classically on fishing effort measured as total pots.

Gotschall (1978b) recently estimated exploitation rates for the Northern California fishery, for the period 1965–72, and obtained estimates ranging from 0.65 to 0.87. Effort levels during this period were high, ranging from 24 000 to 32 000 pots. Assuming a constant instantaneous natural mortality rate (M) of 0.22, one may use Gotschall's estimates of exploitation rates to derive estimates of the instantaneous fishing mortality rate (F) and the catchability coefficient (q) in each year (appealing to classical mortality relations [Ricker 1975]). Applying a mean q for the years considered by Gotschall allows estimation of annual exploitation rates for previous years based upon total pot data. These estimates may be used to extract estimates of year-class strength in past years and to estimate abundance of vulnerable crab at the beginning of each season. Harvest and effort figures used in the following analyses were obtained from PMFC data compilations (PMFC 1977) for the years 1943–68 and from Ron Warner, California Department of Fish and Game, for the years 1969–78.

Division of season landings by the corresponding estimated exploitation rates gives estimates of initial abundance of harvestable crab biomass. Figure 2 illustrates the results of such a reexpression of crab landings as initial abundance figures. Although the apparent cyclic nature of crab abundance remains, the possible increasing amplitude of crab abundance implied by unmanipulated landings figures seems more a reflection of generally increasing fishing effort (and hence exploitation rate) than of actual crab abundance. The pattern of initial abundance appears fairly regular, without an apparent steady upward trend. However, the initial abundance estimates in general reflect contributions from several year-classes of crabs and again do not allow immediate inference of the pattern of year-class strength.

Rough estimates of male crab abundance at age three may be obtained from annual harvest data by: (1) conversion of pounds landed to numbers landed through division by the mean weight in the landings (2.2 lb [Gotschall 1978a]), (2) expression of the numerical harvest in terms of the age-groups that are represented in the harvest, and (3) solution of the derived expression for year-class strength. With estimates of annual exploitation and survival rates for vulnerable males, the annual numerical harvest, H, may be generally expressed as:

$$H(t) = E(t)[R'(t) + S(t-1)R'(t-1) + S(t-1)S(t-2)R'(t-2)], \tag{A}$$

assuming negligible contribution from crabs age 6 and older. Here, E is the exploitation rate, S is the survival rate for vulnerable males, and R' is the initial abundance of age 3 male crabs. Expression (A) may be used to extract estimates of male year-class strength at age 3 assuming that either: (1) exploitation and survival rates for vulnerable males have been constant and equal to 0.85 and 0.10, respectively (as commonly assumed), or (2) these rates have varied with reported fishing effort (as described above). If one assumes constant rates, then expression (A) may be reduced to $H(t) = 0.85R'(t) + 0.085R'(t-1)$, neglecting the minor contribution of older crabs. Given an initial estimate of $R'(t-1)$, $R'(t)$ for successive years may be generated from the available harvest time series. For the variable rate case, initial estimates for $R'(t-1)$ and $R'(t-2)$ are required and, given these, $R'(t)$ for successive years may again be generated from the harvest time series. Since crab harvest for the first available year (1943) was very low, about 10^5 kg, little error is introduced by setting the initial $R'(t-1) = H(1943)/0.85$ for the constant rate case, or $R'(t-1) = R'(t-2) = H(1943)/2E(1943)$ for the variable rate case. The techniques used here are very similar to those presented by Walter and Hoagman (1975).

The abundance of 2-yr-old male and female crab, $R(t)$, may be generated from $R'(t)$ as $R(t) = 2R'(t+1)/0.8$, assuming an equal male:female ratio at age 3 and an annual unexploited survival rate of 0.8. Thus, estimates of crab year-class strength at age 2 may be extracted from landings figures and these estimates depend on the assumed dependence of exploitation and survival rates on fishing effort. These estimates allow direct comparison of fishery data with modeling results and analyses (which will focus on the age 2 life stage) and also allow statistical examination of the "fit" of model variants based on variables generated from landing data.

Generated time series for year-class strength at age 2 (1942–77) were subjected to autocorrelation analysis

TABLE 2. Autocorrelations at indicated lags for extracted estimates of year-class strength at age 2. Year-class strength estimates were obtained assuming either: (1) constant annual exploitation and survival rates for vulnerable males, or (2) variable exploitation and survival rates which depend on fishing effort measured by total pots.

	Autocorrelations	
Lag in years	Constant exploitation rate	Variable exploitation rate
0	1.000	1.000
1	0.596	0.463
2	0.103	−0.023
3	−0.364	−0.336
4	−0.579	−0.619
5	−0.556	−0.567
6	−0.332	−0.329
7	0.117	0.036
8	0.399	0.341
9	0.686	0.528
10	0.726	0.575
11	0.496	0.408
12	−0.015	0.051
13	−0.514	−0.464
14	−0.635	−0.661
15	−0.534	−0.449

to determine whether periodicity apparent in landings was retained also in year-class strength estimates. Largest absolute correlations were found at lags of 4 and 5 yr and 9 and 10 yr, with largest positive correlation at 10 yr (Table 2). The pattern of generated crab year-class strength was thus still cyclic and the probable period was from 9 to 10 yr, probably closer to 10 yr.

Formulation of the Model

We consider an age-stratified population, with $N_n(t)$ denoting the number of individuals of age n (in years) at time t. We suppose that density dependent mechanisms may operate only during the first $M(>0)$ years (the "immature" years) and refer to M as the age of recruitment to the mature stock. During the years of maturity beyond age M, the annual survival rates σ_n are constants, independent of population size or age distribution — though they may depend upon natural environmental factors or upon fishing pressure.

We assume furthermore that during any immature year, if a particular cohort survival rate does depend on population density, only the year-classes of mature animals exert an influence. We finally assume that all mature age-classes exert the same kind of influence, differing only in the intensity of their involvement. Thus the influence of adults on an immature year-class will be expressed through a nonlinear feedback function, dependent on some weighted average of adult numbers.

Let us apply these general considerations to the Dungeness crab. All variants of our model incorporate

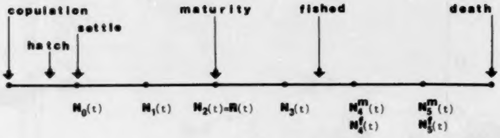


FIG. 3. Life stages, and model designations of life stages, of the Northern California Dungeness crab. Note that there is a full 3-yr lag from copulation of adults until maturity, $R(t)$.

the same basic assumptions, depicted in Fig. 3, concerning the phasing of the life stages of *Cancer magister* in Northern California waters.

We have followed the convention of dating age from the time of settling, and, because of differential survival rates of adult males and females due to the fishery, have kept track of differing male and female numbers from age 4 onward. With $N_n(t)$ denoting the number of age n animals at time t, $N_n{}^m(t)$ the number of males and $N_n{}^f(t)$ the number of females, we assume an effective maternal population at year t

$$N_b(t) = \bar{B}_0 N_2{}^f(t) + \bar{B}_1 N_3{}^f(t) + \bar{B}_2 N_4{}^f(t) + \bar{B}_3 N_5{}^f(t).$$

The weights $\bar{B}_0$, $\bar{B}_1$, $\bar{B}_2$, $\bar{B}_3$ are positive constants which reflect the relative importance of the four age-classes in natality. The manner of choosing these weights will be discussed later (we have considered two alternatives; see Table 3).

The birth and first-year survival of young are now determined by

$$N_0(t+1) = G(N_b(t)),$$

with G a linear or nonlinear natality function. The behavior of the model is powerfully influenced by the form of the feedback function G.

TABLE 3. Summary of model variants.

1. Egg–larval feedback mechanisms
   (B1) Ricker mechanism
   (B2) Beverton-Holt mechanism
   (B3) "Mixed" compensatory mechanism
2. Natality assumptions
   a) 20% of females breed at age 2, 100% breed at ages 3–5
   b) 100% of females breed at age 2, 100% breed at ages 3–5
3. Competition or cannibalism mechanism
   a) Random encounters
   b) Metabolic-related
4. Annual survival rate for adult females and unexploited males
   a) 0.50
   b) 0.80
5. Fishery action
   a) No male harvest
   b) Male harvest (annual survival after age 3 = 0.10)

In most of the subsequent analysis we use the Ricker curve

(B1) $G(N_b) = mN_b\, e^{-\ell N_b}$,

with adjustable parameters ℓ and m, to model density-dependent natality displaying overcompensation. Note that, when $\ell = 0$, G reduces to linear natality. We have also investigated two alternative assumptions about natality and first year survival. We considered compensatory natality dependence, using for this purpose the Beverton-Holt curve

(B2) $G(N_b) = mN_b/[C + N_b]$,

with adjustable parameters C and m. The limiting form of this curve yields constant recruitment, m. Finally, we considered a "mixed" natality feedback mechanism

(B3) $G(N_b)F_0(N_d) = mN_b\, e^{-k_0 N_d}$.

This has egg production proportional to effective adult female numbers N_b, but modified downward from this potential by the exponential $e^{-k_0 N_d}$, which reflects "crowding" involving both male and female numbers: N_d is an effective compensatory adult population (acting through cannibalism or competition)

$$\begin{aligned} N_d(t) = {} & \bar{D}_0{}^m N_2{}^m(t) + \bar{D}_1{}^m N_3{}^m(t) + \bar{D}_2{}^m N_4{}^m(t) \\ & + \bar{D}_3{}^m N_5{}^m(t) + \bar{D}_0{}^f N_2{}^f(t) + \bar{D}_1{}^f N_3{}^f(t) \\ & + \bar{D}_2{}^f N_4{}^f(t) + \bar{D}_3{}^f N_5{}^f(t). \end{aligned}$$

Alternative assumptions for determining the weights $\bar{D}_n$ are listed in Table 3 and are discussed below.

We note that this third feedback mechanism may be used for direct comparison of our model ouput with that of Botsford-Wickham, since like the mechanism in their (continuous) model, this one involves no lag between the application of N_b and N_d.

Survival through juvenile years may also be density-dependent; indeed predation by adults on juveniles has been considered a likely important negative feedback control (Botsford and Wickham 1978). We model this possibility by putting

$$N_1(t + 1) = N_0(t) \quad F_1[N_d(t)],$$

$$N_2(t + 1) = N_1(t) \quad F_2[N_d(t)],$$

with the density-dependent survival rates F_j given by the negative exponential

(D1) $F_j(N_d) = \delta_j\, e^{-k_j N_d}, \qquad j = 1, 2.$

The constants δ_j, k_j are adjustable parameters; when $k_j = 0$ one gets density-independent mortality

$$F_j(N_d) = \delta_j$$

Finally, density-independent survival of adults is expressed by

$$N_2{}^m(t) = N_2{}^f(t) = \tfrac{1}{2}N_2(t)$$

$$N_3(t + 1) = N_2(t)\sigma; \qquad N_3{}^m(t) = N_3{}^f(t) = \tfrac{1}{2}N_3(t)$$

$$N_4{}^m(t + 1) = N_3{}^m(t)\sigma^m; \quad N_4{}^f(t + 1) = N_3{}^f(t)\sigma^f$$

$$N_5{}^m(t + 1) = N^m{}_4(t)\sigma^m; \quad N_5{}^f(t + 1) = N_4{}^f(t)\sigma^f.$$

Here, the separate male and female survival rates σ^m and σ^f, applied in the 4th and 5th years since copulation, reflect the differential effects of fishery mortality. In our models we have chosen to ignore the older age groups N_6, N_7, etc., assuming that they exert only a modest influence on population processes.

In a given year, age-group numbers for mature animals beyond age 2 may be calculated (in terms of the σ's) directly from recruited numbers $R = N_2$ in the preceding years, and then these may be used to calculate future recruitment through the chain of density dependence. Thus the system of equations reduces to a single equation of nonlinear renewal type (e.g. Feller 1968), expressing $R(t)$ in terms of R at earlier times:

$$\begin{aligned} R(t) = {} & G[R_b(t - 3)]F_0[R_d(t - 3)]F_1[R_d(t - 2)] \\ & \times F_2[R_d(t - 1)] \end{aligned}$$

where

$$\begin{aligned} R_b(t) = {} & B_0R(t) + B_1R(t - 1) + B_2R(t - 2) \\ & + B_3R(t - 3) \end{aligned}$$

and

$$\begin{aligned} R_d(t) = {} & D_0R(t) + D_1R(t - 1) + D_2R(t - 2) \\ & + D_3R(t - 3). \end{aligned}$$

The positive constants B_n, D_n may be calculated easily from the $\bar{B}_n$, $\bar{D}_n$, and σ's above.

An equilibrium solution $R(t) \equiv R^*$ of the renewal equation has to satisfy

$$R^* = G(BR^*)F_0(DR^*)F_1(DR^*)F_2(DR^*) \equiv G^*F_0{}^*F_1{}^*F_2{}^*$$

with

$$B = B_0 + B_1 + B_2 + B_3 \text{ and } D = D_0 + D_1 + D_2 + D_3.$$

Graphical solution of the equilibrium equation for our three models, (B1) or (B2) or (B3), with (D1), is analogous to that for the standard stock-recruitment models. In each case there is a unique equilibrium (which may be unstable in some parameter regions).

The equilibrium $R(t) \equiv R^*$ is given in the three cases by the following implicit relations:

For the overcompensatory model, (B1) with (D1),

$$\frac{1}{B} = \delta\, e^{-\gamma R^*}, \quad \text{where} \quad \delta = m\delta_1\delta_2$$

and

$$\gamma = B\ell + D(k_1 + k_2).$$

For (B3) with (D1),

$$\frac{1}{B} = \delta\, e^{-\gamma R^*}, \quad \text{where} \quad \delta = m\delta_1\delta_2$$

and

$$\gamma = D(k_0 + k_1 + k_2).$$

For the Beverton-Holt model, (B2) with (D1),

$$\frac{C}{B} + R^* = \delta\, e^{-sR^*}, \quad \text{where} \quad \delta = m\delta_1\delta_2$$

and

$$s = D(k_1 + k_2).$$

The weights $\bar{B}_n$ and $\bar{D}_n$ and survival rates δ — Assumptions about $\bar{B}_n$ and $\bar{D}_n$ involve the age of first reproduction and the possible mechanisms which might govern competition or cannibalistic behavior by adult crabs. Since it is not clear that all female Dungeness crab breed upon first reaching maturity at age two (D. Wickham, Bodega Marine Laboratory, Univ. of Calif., Bodega Bay, CA 94923, personal communication), we determined $\bar{B}_n$ by assuming either that (1) all females breed at age 2 or (2) only 20% breed at age 2. In all cases we assumed that 100% of female adults age 3 and older breed each year. Estimates of $\bar{B}_n$ are proportional to the product of the percent reproduction at age and the age-specific fecundity (Botsford and Wickham 1978), adjusted so that $\bar{B}_3 = 1$. Assumed age-specific fecundities at ages 2 through 5 were (in millions of eggs): 0.75, 1.30, 1.60, and 2.20.

At least two possible mechanisms might govern cannibalism by adults on juveniles. Cannibalism could be on a random encounter basis (Ricker 1954), where the probability of a juvenile crab surviving cannibalism depends on the total numerical density of adult crabs. Or cannibalism could be related to the food maintenance requirements of adult crabs, which is proportional to the age and sex-specific weight raised to the 0.8 power (Warren 1971). Estimates of $\bar{D}_n$ differ according to the above alternatives in that greater weight is given to older, larger, male adults under the maintenance requirement assumption while equal weight ($\bar{D}_n = 1$) is given all adult crabs under the random encounter alternative. Weight at age data (Butler 1960) was used to determine $\bar{D}_n$ estimates for the maintenance requirement assumption. $\bar{D}_0$ was set equal to one and other $\bar{D}_n$ were expressed relative to $\bar{D}_0$. The same alternatives for $\bar{D}_n$ served in specifying crowding effects in the "mixed" natality mechanism (B3).

Uncertain estimates of adult crab survival rates were reflected in model variants by allowing σ^f, the survival rate for adult females (and for males in unexploited populations), to take on the values 0.8 and 0.5. For all models of exploited populations we let σ^m, the survival rate for exploited males, equal 0.1, reflecting an annual exploitation rate of about 0.85. We also undertook model simulations in which σ^m was variable, reflecting historic effort levels.

Finally, before analysis and simulation is possible, the parameters involved in the F functions (δ_i, k_i) must be determined. The same assumptions are made for all models. We let $\delta_1 = 0.5$ and $\delta_2 = 0.8$, reflecting increased maximum juvenile survival rate with age, and assume that $k_1 = k_2$ to simplify model analyses and simulations. There is an arbitrariness in this, since the model actually determines total mortality across all prerecruitment years.

The parameter m in the natality functions (B1), (B2), or (B3) determines, or is determined by, the equilibrium population level R^*. In our simulations we have chosen to normalize m so as to obtain an equilibrium $R^* = 1$ when males are exploited to a 0.1 annual survival. The equilibrium resulting with an unexploited population or a female-harvested population is then simply a relative number.

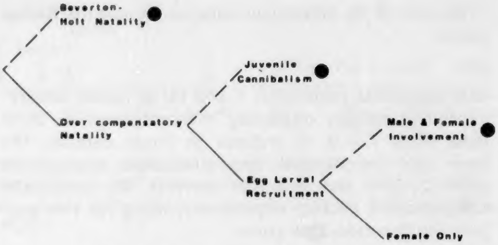


FIG. 4. Schematic of the process of elimination technique employed to evaluate plausible control mechanisms. Dashed lines lead to mechanisms rejected as implausible for reasons stated in text.

Model Waveform Analysis

The ultimate purpose of the analysis is to determine which, if any, of the model variants summarized in Table 3 can generate population patterns consistent with the empirical time series, and in particular to assess the timing and intensity of feedback mechanisms which can achieve this. Our diagnostic test is to look for persistent stable population cycles, and to examine their period and waveform. In this way we shall be able successively to eliminate almost all model alternatives, narrowing down finally to a single one or two. The process is summarized graphically in Fig. 4, and will be worked out in detail below.

The logic of the elimination process demands that one must show not only that a certain model variant can produce acceptable output but also that the other variants cannot. This necessitates an analysis of stable cycling phenomena in all model variants.

LINEAR STABILITY ANALYSIS

We have already noted that all variants of the model possess a steady state equilibrium solution $R(t) \equiv R^*$. However it is important to ascertain the stability of that equilibrium, i.e. whether a population when displaced from equilibrium tends to return to it. This, as we will see, depends strongly on the nature and intensity of the biological feedback mechanism, embodied in the functions G and F, and measured through the constants ℓ and k in formulas (B1-3) and (D1).

Linear stability analysis examines *small* perturbations $r(t) = R(t) - R^*$ around the equilibrium (May 1973). Setting $v(t)$ equal to the variation (linear approximation) of $r(t)$, then $v(t)$ satisfies the variational equation

$$v(t) = \eta_b v_b(t-3) + \eta_{d_0} v_d(t-3) + \eta_{d_1} v_d(t-2) + \eta_{d_2} v_d(t-1),$$

where v_b and v_d are defined analogously to R_b and R_d:

$$v_b(t) = B_0v(t) + B_1v(t-1) + B_2v(t-2) + B_3v(t-3),$$

$$v_d(t) = D_0v(t) + D_1v(t-1) + D_2v(t-2) + D_3v(t-3),$$

and the coefficients η are (for $j = 0, 1, 2$)

$$\eta_b = R^*G'(BR^*)/G(BR^*);$$

$$\eta_{d_j} = R^*F_j'(DR^*)/F_j(DR^*).$$

Note the simple geometrical interpretation of the coefficients: For example, $B\eta_b$ is the ratio, at the point BR^* on the natality curve G, of

(Slope of tangent line) / (Slope of chord to origin).

In particular, η_b is negative when BR^* lies under the decreasing branch of an overcompensatory G. (The Ricker model, B1). The constants η_{d_j} are always negative (from D1) whenever there is compensatory mortality. (They are zero in the absence of feedback, i.e. when $k = 0$).

Solving the variational equation reduces to finding the roots of the corresponding characteristic equation

$$\text{(C)} \quad \lambda^6 = \eta_b \sum_{j=0}^{3} B_j\lambda^{3-j} + \sum_{i=0}^{2} \eta_{d_i} \sum_{j=0}^{3} D_j\lambda^{3+i-j}.$$

Each characteristic root λ provides a solution $v(t) = = \lambda^t$ of the variational equations and, in the usual case where the six roots of the polynomial are all distinct, their linear combinations give all possible variations $v(t)$. Complex conjugate pairs of roots $\lambda_\pm = \rho[\cos\theta \pm i\sin\theta]$ give rise to oscillatory variations

$$v(t) = \rho^t \cos t\theta \quad \text{or} \quad v(t) = \rho^t \sin t\theta,$$

of period $2\pi/\theta$.

In case every characteristic root satisfies $|\lambda| < 1$ (i.e. $\rho < 1$ in the complex case), then $v(t) \rightarrow 0$ as $t \rightarrow \infty$ and the linearized theory implies (correctly) that

$$R(t) \rightarrow R^* \quad \text{as} \quad t \rightarrow \infty,$$

i.e. the equilibrium R^* is (locally) stable.

However, when $|\lambda| > 1$ for some characteristic root, so that the corresponding variation $v(t)$ "blows up," i.e.

$$|v(t)| \rightarrow \infty \quad \text{as} \quad t \rightarrow \infty,$$

then the linear theory is no longer a reliable indication of the true behavior of the solution $R(t)$ of the nonlinear renewal equation. (Indeed, the variational equation was derived under the assumption that $v(t)$ remains small.)

Now, the coefficients in the characteristic equation, and from them the nature of the characteristic roots, of course depend on the parameter values in the original population dynamic equations. In particular, the coefficients η_b and η_{dj} depend on the values of the parameters k and ℓ, and so reflect the timing and intensity of the feedback mechanism.

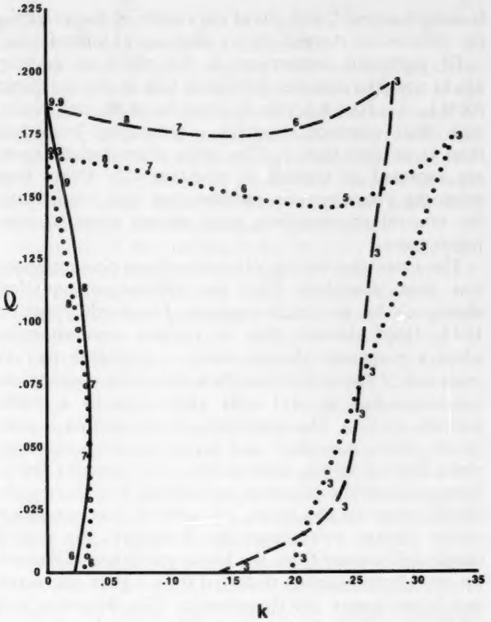


FIG. 5. Linear stability diagram illustrating stability boundary and linear estimates of period at boundary for exploited and unexploited states of two model variants: solid and dashed lines — unexploited and exploited boundaries for Ricker model (B1) variant with 2a), 3b), and 4b); solid-open dots and dotted line — unexploited and exploited boundaries for Ricker model (B1) variant with 2b), 3b), 4b). Refer to Table 3 for description of variants. The diagram shows k, ℓ-parameter space, where k is the intensity of juvenile mortality feedback, and ℓ is the intensity of natality and larval mortality feedback. In each case, the stable region is below and to the left of the stability boundary.

It is therefore instructive to display graphically the influence of those two parameters on stability (while holding fixed all other population parameter values). Figure 5 is a stability diagram in k, ℓ-parameter space. Each point in this space represents a particular assumption about feedback intensity; hence, different points represent essentially different variants of the model. The stability boundary Γ marks the transition between a region of parameter space where the steady-state equilibrium is linearly stable (because all characteristic roots satisfy $|\lambda| < 1$) and a region where this property fails (because certain $|\lambda| > 1$).

One can envision the six characteristic roots as a set of points in a complex plane, points which move continuously as the parameter pair (k, ℓ) is vaired in parameter space. If we imagine (k, ℓ) to be initially in the stable region, then the corresponding six characteristic roots all lie within the unit disc $|\lambda| < 1$. As (k, ℓ)

is moved across Γ and out of the region of linear stability, then one or more of the λ's cross out of the unit disc.

Of particular importance is the effect of varying (k, ℓ) so that a complex conjugate pair of characteristic roots $\lambda_{\pm} = \rho\ (\cos\theta \pm \mathrm{i}\sin\theta)$ cross out of the unit circle, with their common modulus ρ increasing from less than to greater than 1. The other characteristic roots are assumed to remain in modulus <1. (Note that since the characteristic equation has real coefficients, the nonreal characteristic roots always come in conjugate pairs.)

The true behavior of $r(t)$ under these circumstances was first described (for the differential equation analogue) by the mathematician Eberhardt Hopf in 1942. Hopf showed that, in certain circumstances, when a parameter change causes a conjugate pair to cross out of the unit circle, then the stable equilibrium (corresponding to $r(t) \equiv 0$) gives over to a stable periodic motion. The amplitude of this motion is zero on the stable boundary and grows as the parameters move beyond it but, unlike $v(t)$, $r(t)$ remains finite. The period of the motion is very nearly $T = 2\pi/\theta$ sufficiently close to the boundary, and as the parameter values change away from the boundary, the period slowly drifts away from the linear prediction. Likewise the waveform becomes distorted from a pure sine wave and is no longer strictly periodic. (See Marsden and McCracken 1976, Section 6 on diffeomorphisms.)

On the stability diagram, Fig. 5, we have shown not only the location of the stable boundary, but also the linear estimate of period T, calculated from the dominant pair of complex conjugate characteristic roots for which $|\lambda_{\pm}| = 1$. It will be noted that for the model variant being considered (the Ricker model, B1, with cannibalism of juveniles, D1) periods of length 9 or 10 yr do occur, but only when the juvenile compensatory feedback mechanism is very weak, i.e. k is small. (Recall that the empirical landings time series and the year-class strength estimates extracted from it both have periods of 9–10 yr.)

Figure 5 is of course a special case, in that the population parameters (other than k and ℓ) have been assigned particular values, from Table 3. But the same essential features are seen when one tests other values of the secondary parameters (see Fig. 6, 7). Compensatory mortality must act in the first year of life and must be weak (or absent) in juvenile years; otherwise cycles of period 9–10 yr are impossible. (A variant, not tested, would concentrate negative feedback in the first juvenile year, i.e. $k_1 \gg k_2 \geq 0$. But that case would be intermediate between the one just described and the mixed model whose performance, including certain unacceptable features, is described below.) The Beverton-Holt model allows cycles of no longer than seven years; indeed, by a general argument, no model for which η_b is positive can do otherwise.

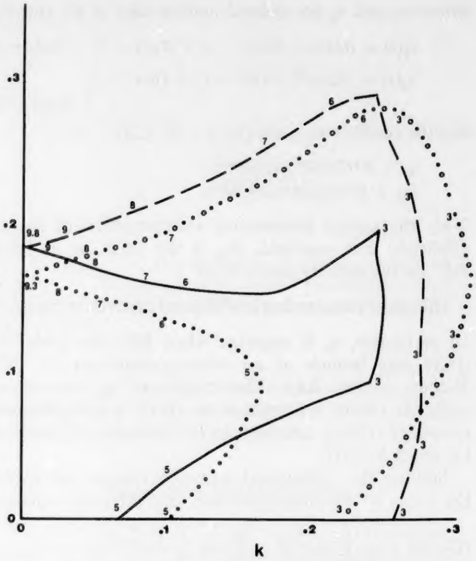


FIG. 6. Linear stability diagram illustrating stability boundary and linear estimates of period at boundary for exploited and unexploited states of two model variants: solid and dashed lines — unexploited and exploited boundaries for Ricker model (B1) variant with 2a), 3a), 4b); dotted line and solid-open dots — unexploited and exploited boundaries for Ricker model (B1) variant with 2b), 3a), 4b). Refer to Table 3 for description of model variants. The diagram shows k, ℓ-parameter space, where k is the intensity of juvenile mortality feedback, and ℓ is the intensity of natality and larval mortality feedback.

It is instructive to utilize the linear analysis to infer the effect of fishing pressure on the equilibrium population level and stability of the models. In overcompensatory birth models (B1) or (B3), equilibrium population R^* satisfies

$$\frac{1}{B} = \delta\, \mathrm{e}^{-\gamma R^*}, \quad \delta = m\delta_1\delta_2, \quad \gamma = B\ell + D(k_0 + k_1 + k_2)$$

and the coefficients η_b and η_{d_j} are

$$\eta_b = (1 - \ell BR^*)/B \quad \text{and} \quad \eta_{d_j} = -k_j R^*, \quad (j = 0, 1, 2).$$

One incorporates the change from an unexploited male population to an exploited one by decreasing the adult male survival rate σ^m (from 0.8 to 0.1 in some calculations) and thereby decreasing D_1, D_2, D_3, and D. (The basic biological parameters m, ℓ, δ, k, and natality parameters B_n are unchanged). As a result, the overall Ricker constant γ decreases under fishing pressure, so that (since γR^* is constant) the equilibrium population R^* rises. Both η_b and η_{d_i} are decreased (in the case of η_{d_i}, made more negative), but the effect upon the modulus of eigenvalues is complicated and no generalizations are evident. The largest $|\lambda|$ may increase or decrease; however, numerical solution of the characteristic equation (C) shows that the usual effect of exploitation in the relevant parameter ranges is to

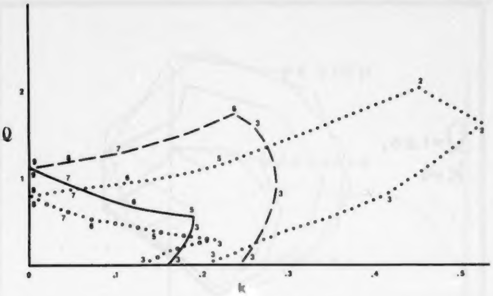


FIG. 7. Linear stability diagram illustrating stability boundary and linear estimates of period at boundary for exploited and unexploited states of two model variants: solid and dashed lines — unexploited and exploited boundaries for Ricker model (B1) variant with 2a), 3b), 4a); solid-open dots and dotted line — unexploited and exploited boundaries for Ricker model (B1) variant with 2b), 3b), 4a). Refer to Table 3 for description of model variants. The diagram shows k, ℓ-parameter space, where k is the intensity of juvenile mortality feedback, and ℓ is the intensity of natality and larval mortality feedback.

decrease $|\lambda|$, i.e. to stabilize cyclic variations or even to damp them out. (Note that if, as suggested by the 9–10 yr period, the value of k must be small, then the effect of male harvest in the Ricker model (B1) must also be small; if $k = 0$ male harvest will have no effect on either equilibrium R^* or cycle period.)

If one uses the Beverton-Holt natality function, similar effects are seen. Equilibrium occurs at R^* where

$$\frac{C}{B} + R^* = \delta\, e^{-sR^*}; \quad \delta = m\delta_1\delta_2, \quad s = D(k_1 + k_2)$$

and

$$\eta_b = \frac{1}{B\left(1 + \frac{B}{C}R^*\right)} \geq 0, \quad \eta_{d_\ell} = k_\ell R^*.$$

The effect of exploitation again is to increase R^* and to decrease η_b and η_{d_ℓ}; however now η_b must remain positive.

NONLINEAR ANALYSIS

We turn next to a more careful investigation of the model behavior in the parameter region of greatest interest, the region beyond the stable boundary, where persistent population cycles are expected.

Mathematical methods exist (more completely worked out for differential equations than for difference equations) to calculate iteratively the qualitative features of the limit cycle and to check the nature of the stability. However, for an ordinary difference equation it may be simpler and more accurate to resort to simulation to investigate these things — once one has solved the characteristic equation and hence has located the stable boundary. We take this approach below in our analysis of the Dungeness crab model.

A difficulty in analyzing periodicities through simulation arises because of the high order (here 6) of the difference equation. The population trajectory must be thought of as a six-dimensional vector $\mathbf{X}(t)$, with one component $X_k(t)$ corresponding to each age-class $k = 0, 1, \ldots, 5$. To follow the population changes through time, one must track the motion of the population vector through six-dimensional "phase space."

Fortunately, the limiting behavior (as $t \to \infty$) of the population trajectory is considerably simpler. According to the Center Manifold Theorem (see Marsden and McCracken), for parameter values near the stable boundary, the population trajectory is attracted, as $t \to \infty$, to a certain two-dimensional curved surface in the six-dimensional space. Thus, the population trajectory is asymptotically only two-dimensional. One can observe the population trajectory most clearly by projecting its points down onto the attracting manifold, or onto its tangent plane at the equilibrium point R^*. The details of how this may be done are developed in Appendix 1, and the process is illustrated in the simulation for the Dungeness crab model.

One finds that there is a comparatively narrow band in k, ℓ-parameter space within which stable cycles occur. Crossing the band, beginning at the stable boundary, oscillations which are initially quite mild grow more intensive. Figure 8 shows time plots of the oscillations in $R(t)$ for a sequence of parameter points stepping across the band. A more accurate appraisal is obtained by examining the phase-plane portraits at these same parameter points (Fig. 9). Nearest the stable boundary, a closed loop (seen in projection on a strategically chosen plane in six-dimensional phase space) is traversed repeatedly over time. The period of traverse is not an integer number of years; therefore, each time around the points advance a little, and over many cycles the curve is filled in solidly. By following the process closely, one can accurately appraise the period (number of years t divided by number of complete traversals when t is large) as well as the amplitude of cycling. The results for period and amplitude are plotted in k, ℓ-parameter space in Fig. 10a, 10b, and 11.

Eventually, with a sufficient change in parameters away from the stable boundary, the cyclic trajectory itself becomes only quasi periodic; the loop does not repeat precisely. Beyond the band, repeated bifurcations lead to a motion which is wholly chaotic in appearance and indistinguishable from that which would result from random environmental fluctuations. This property of discrete models has received much attention in the recent ecological literature (May and Oster 1976; Guckenheimer et al. 1977), but we will not deal with it here. Rather we wish to focus on populations (such as the Dungeness crab) where periodicity is strongly evident and wave forms are comparatively simple, so that an initial Hopf bifurcation gives promise of providing a suitable model.

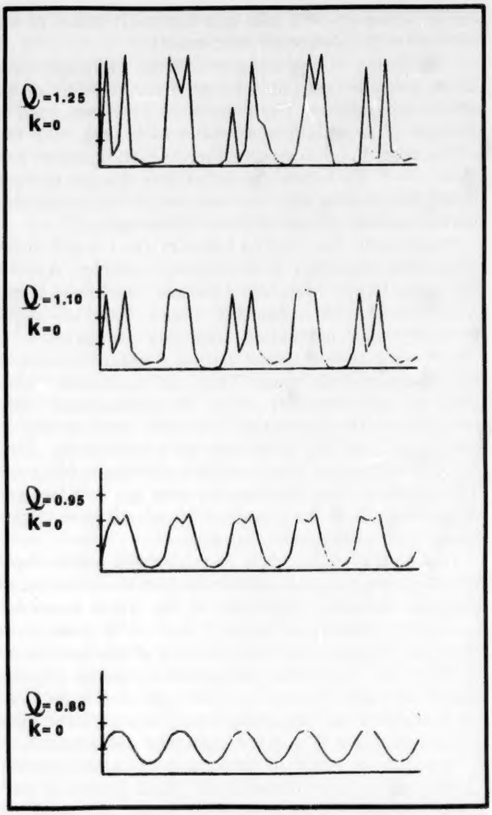


FIG. 8. Time-plots of $R(t)$ for parameter values crossing stable boundary toward region of unstable cycling. For Ricker model (B1) with 2a), 3b), 4a). Refer to Table 3 for description of model variant.

Quite evidently, the empirical evidence from the Dungeness crab landings is consistent with this condition. Indeed, it seems possible that chaotic population dynamics are rare in natural systems generally. Hassell, et al. (1976) surveyed some 28 data sets on insect populations and found no example of a natural population having parameter values in a chaotic regime, though some laboratory populations had. Tanner (1975), in examining predator–prey systems, found none (and only one that cycled). Of course, the most likely explanation of erratic natural population fluctua-

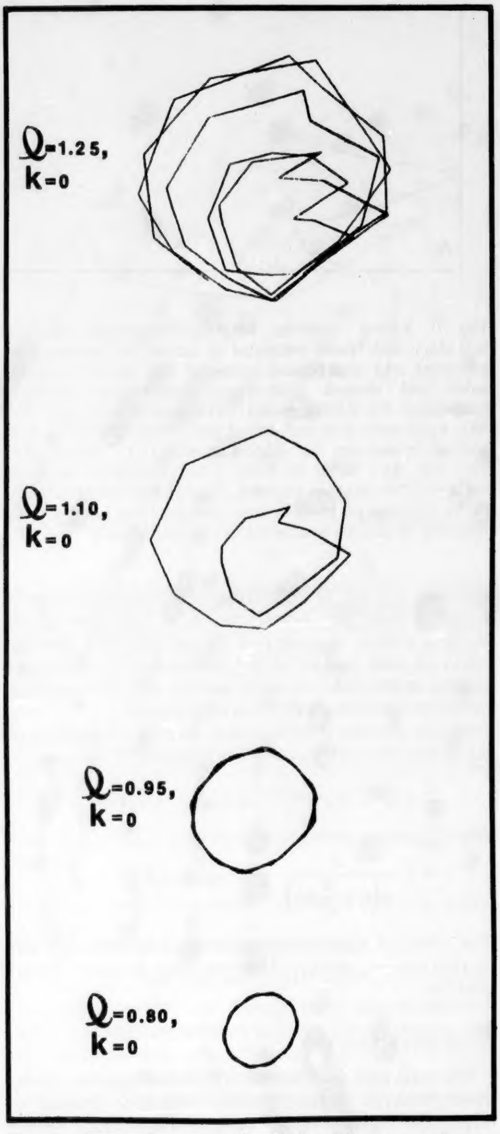
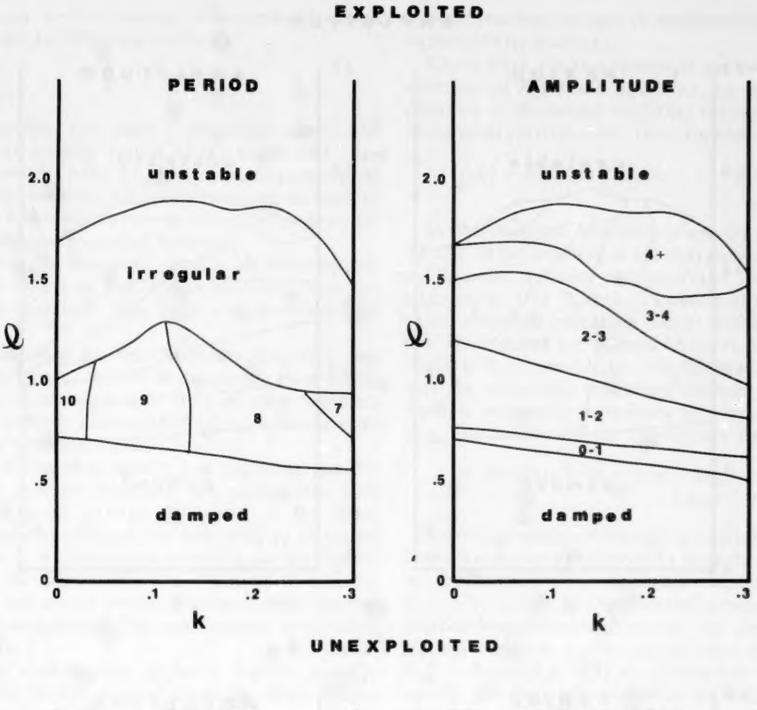


FIG. 9. Phase-plane portraits of closed loops seen in projection. Same parameter values and model variant as for Fig. 8.

FIG. 10a. Nonlinear estimates of period and amplitude in regions of stable cycling, and boundaries of stable and unstable behavior for exploited and unexploited states of Ricker model (B1) with 2a), 3b), 4b). Model behavior was assessed from simulations of 16 complete cycles after population had been "run" for 200 yr. Behavior is characterized as "unstable" when $R(t)$ is less than 0.0025 or becomes larger than 250. Period is assessed by interval length between successive crossings of the normalized equilibrium line, $R(t) = 1$.



"Irregular" regions indicate that produced time series are of sufficiently complex patterns to frustrate period detection by the above method. "Amplitude" is determined as: (average maximum − average minimum)/2, computed over 16 cycles. Refer to Table 3 for description of model variant.

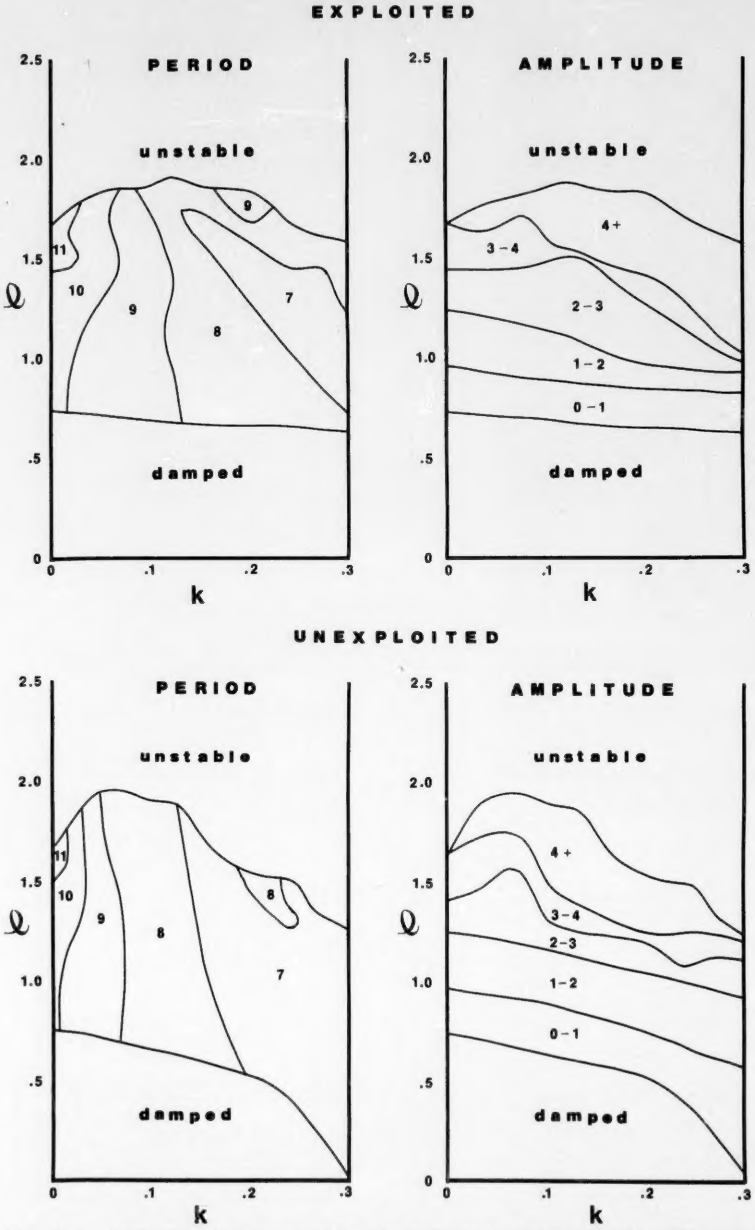


FIG. 10b. Nonlinear estimates of period and amplitude in regions of stable cycling, and boundaries of stable and unstable behavior for exploited and unexploited states of Ricker model (B1) with 2a), 3b), 4b) (as in Fig. 10a). Criteria for characterizing model behavior is as for Fig. 10a except, the phase plane projection technique has been employed. Note

tions continues to be random environmental effects rather than chaotic biological feedback.

CONCLUSIONS

Taken together, the general discussion above and the numerical stability results (both linear and nonlinear) provide the basis for the elimination process of Fig. 4. To summarize: All model variants do lead to stable cycles of simple waveform when one chooses appropriate feedback intensities. However:

1) Only overcompensatory natality can yield periods of cycling in excess of 7 yr, a fact following from the characteristic equation. This rules out Beverton-Holt natality.

2) By examining the linear stability diagrams, one concludes that even with overcompensatory natality, the presence of any substantial juvenile stage feedback will shorten periods unacceptably. This result is reinforced by the nonlinear stability analysis.

3) Both a Ricker-type natality and the mixed model's male–female natality feedback are compatible with periodic cycling of 9–10 yr. However, in the latter model the period is substantially depressed by increased male harvest — a phenomenon which seems inconsistent with the historical pattern. (It is worth noticing also that in the mixed model, increased male harvest tends to be destabilizing. This runs counter to all other model variants.)

4) Finally, examination of the k, ℓ-plane stability properties with Ricker natality shows that there is little sensitivity in the model to variations in percentage breeding at age 2 or annual adult survival rates (see Table 3). Nevertheless the best fit (which we have used in "fine tuning") seems to come by assuming

20% of the females breed at age 2
0.8 is the annual survival rate for adult females and unexploited males.

Under these assumptions, the nonlinear stability period analysis implies

$$0 < k < \sim 0.1 \qquad 0.75 < \ell < 0.90.$$

Model Regression Analysis

The conclusions of the stability analysis of the previous section are reinforced by more traditional curve fitting approaches for evaluation of the density-dependence parameters (m, ℓ, k_0, k_1, k_2). While regression analysis does not give insight into the qualitative behavior of the rejected model variants, it does add precision in fitting the historical time series, since the past variability in fishing effort may easily be incorporated into calculations. This is especially valuable for assessing the parameters of the "mixed" model (and was not possible, because of mathematical intractability, in the stability analysis).

Given $R(t)$, the recruitment at age two in our model, estimates of $R_b(t)$ and $R_d(t)$ may be generated by application of the model weighting functions, $\bar{B}_n$ and $\bar{D}_n$, and annual survival rates. Thus, for example:

$$R_b(t) = \bar{B}_0R(t) + 0.8\bar{B}_1R(t-1) + 0.8^2\bar{B}_2R(t-2) + 0.8^3\bar{B}_3R(t-3).$$

In this fashion, estimates were obtained for both 20 and 100% breeding at age two variants (for $R_b(t)$), and for both random encounter and food competition alternatives (for $R_d(t)$). Two sets of estimates were again obtained, reflecting either constant or variable rate assumptions for vulnerable males. Given estimates of $R(t)$, $R_b(t)$, and $R_d(t)$, the full model, B1 with D1, may be statistically examined through application of multiple regression techniques to a model transformation. For this model the appropriate transformation is

$$\ln [R(t)/R_b(t-3)] = \ln m - \ell R_b(t-3) - k_1R_d(t-2) - k_2R_d(t-1).$$

Results of multiple regression analysis of this transformation showed that from 83 to 86% of the variation in the transformed dependent variable, $\ln [R(t)/R_b(t-3)]$, could be explained by regression on all three independent variables. However, the decrease in unexplained variation due to the addition of the variables $R_d(t-2)$ and $R_d(t-1)$ was always less than 1.5% and usually less than 1%, regardless of weighting function variant or assumptions regarding rates for vulnerable males. A negligible statistical relation between the dependent variable and the two variables reflecting possible cannibalism by adult crabs on juveniles is inferred. Thus, the modeling conclusion that year-class strength is determined primarily in the period egg-to-settling is supported by multiple regression analysis.

If the influence of adult crab upon juvenile crab beyond the age 0 stage is negligible, the full model may be reduced to a simpler model relating year-class strength to adult densities three years previous. In this case there are two plausible models worth examining: model **B1** (the age-structured Ricker curve) and model **B3** (the mixed feedback model). In reduced form these models may be written as:

$$\text{B1}': R(t) = mR_b(t-3)\,e^{-\ell R_b(t-3)},$$

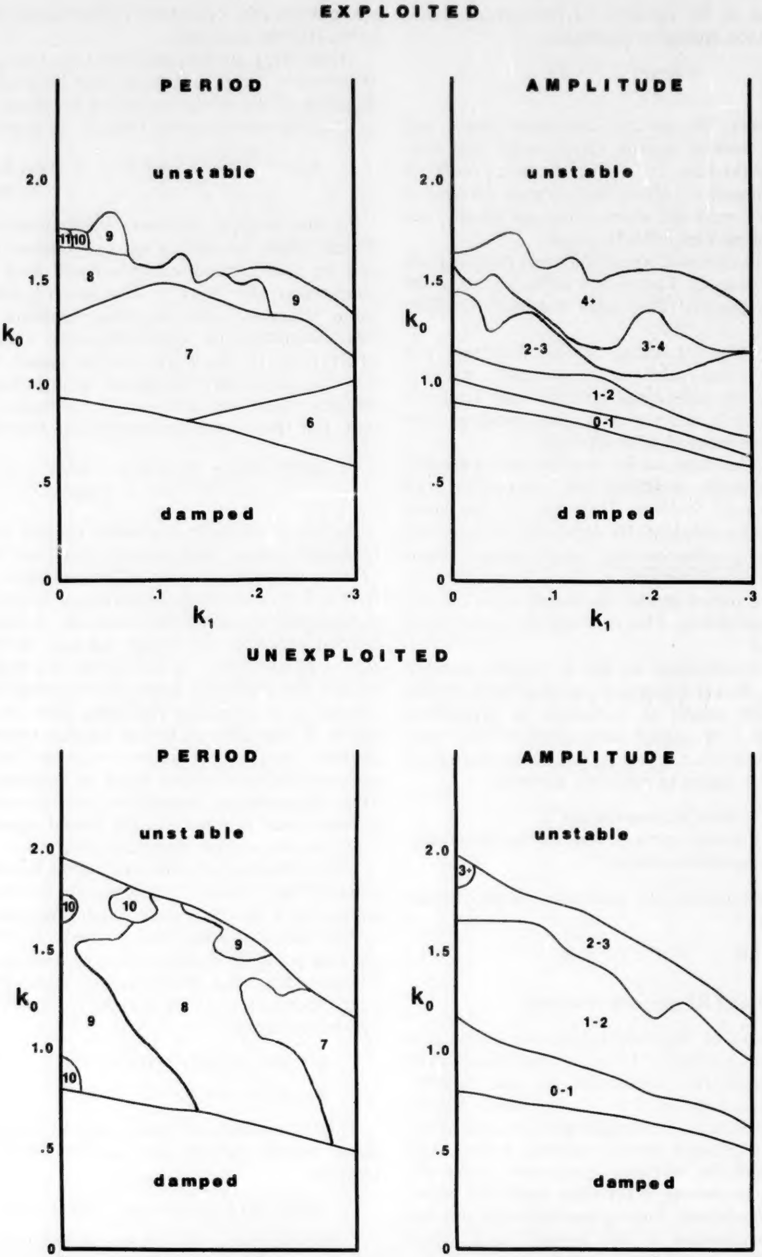
$$\text{B3}': R(t) = mR_b(t-3)\,e^{-k_0R_d(t-3)}.$$

Transformations of these reduced models produce linear models suitable for standard linear regression analysis:

$$\ln [R(t)/R_b(t-3)] = \ln m - \ell R_b(t-3),$$

$$\ln [R(t)/R_b(t-3)] = \ln m - k_0R_d(t-3).$$

that the region of irregular cycling is eliminated and that periodic behavior may be assessed in parameter space regions further from the stable boundary.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0-1
damped
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UNEXPLOITED
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3+
2-3
1-2
0-1
damped

TABLE 4. Linear and nonlinear regression analysis results for the Ricker model, B1′. The estimates of ℓ obtained from regression have been adjusted to a normalized year-class strength of one by: $\ell^* = \ell \times (X_0/1)$, where X_0 = equilibrium year-class strength at age two based on estimated parameters, m and ℓ.

Assumptions: Regression technique	Estimates				
	m	ℓ	ℓ^*	X_0	R^2
Constant exploitation and survival rates					
20% females breed age 2:					
Linear	5.468	0.116	0.938	8.09	0.837
Nonlinear	4.559	0.098	0.878	8.96	0.803
100% females breed age 2:					
Linear	4.816	0.101	0.810	8.02	0.829
Nonlinear	3.886	0.084	0.745	8.87	0.818
Variable exploitation and survival rates					
20% females breed age 2:					
Linear	6.166	0.103	0.980	9.51	0.850
Nonlinear	4.346	0.082	0.862	10.51	0.822
100% females breed age 2:					
Linear	5.458	0.090	0.842	9.36	0.837
Nonlinear	4.011	0.074	0.759	10.26	0.850

However, as Sissenwine (1978) recently pointed out, transformation of a model similar to B1′ is likely to yield a significant linear correlation even when the original model variables (here $R(t)$ and $R_b(t-3)$) are completely uncorrelated. To protect against this possibility, alternative estimates of m and ℓ were obtained by nonlinear least-squares regression (Draper and Smith 1966), without transformation, for comparison with the linear least-squares estimates. The nonlinear least-squares criterion is to minimize

$$\Sigma[R(t) - \hat{m}R_b(t-3)\, e^{-\hat{\ell}R_b(t-3)}]^2,$$

where $\hat{m}$ and $\hat{\ell}$ are estimates of the "true" parameters m and ℓ. Assumed distribution of error does, of course, differ according to the regression technique.

The results of both linear and nonlinear regression analyses of model B1′ are presented in Table 4. Nearly 85% of the variation in the dependent regression variable could be explained by regression on $R_b(t)$ by either regression technique for both constant and variable rate assumptions used to derive year-class strength estimates. Year-labeled graphs (Fig. 12, 13) of the transformed variables show apparent cyclic patterns with a period of 9 or 10 yr and strong negative relations between the natural logarithm of the dependent variable (analogous to survival from egg to age 2) and the female parent stock. Estimates of ℓ, adjusted for the ratio of estimated equilibrium year-class strength to the normalized level of 1 used in stability analyses, ranged from about 0.75 to 1.0. These values are remarkably close to the range of ℓ, roughly 0.75–0.90, suggested as reasonable by simulations (refer to Fig. 10a and 10b).

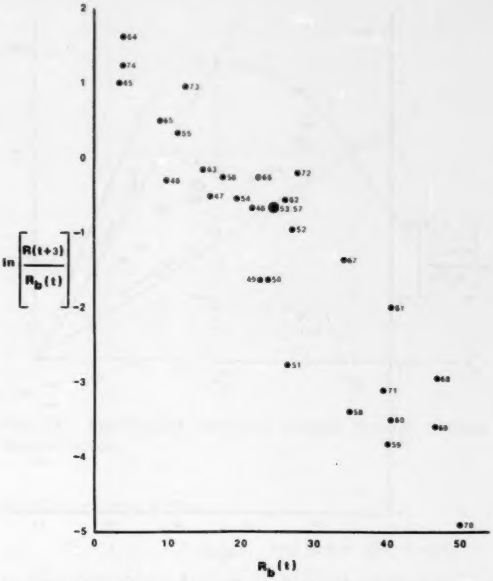

FIG. 12. Year-labeled linear transformation of Ricker model (B1) relating extracted year-class strength estimates (R) to estimated parent stock egg capacity (R_b). Based on extracted year-class strength estimates assuming that exploitation and survival rates vary classically with total pot data. Assumes 20% of females breed at age 2 and an annual unexploited survival rate of 0.80.

Linear least-squares regressions of the transformed "mixed" model, B3′, failed to indicate as strong a relation between the dependent variable (the same as for model B1′) and $R_d(t)$, a measure of adult density involving both males and females. From 55 to 75% of the variation in the dependent variable could be explained by regression on $R_d(t)$.

Estimates of k_0, adjusted as above, ranged from about 1.0 to 1.3. Reference to Fig. 11 shows that these values

FIG. 11. Nonlinear estimates of period and amplitude in regions of stable cycling, and boundaries for stable and unstable population behavior for exploited and unexploited states of the "mixed" model (B3) with 2a), 3b), 4b). Criteria for characterizing model behavior is as for Fig. 10b); the phase plane projection technique has been employed. Refer to Table 3 for description of model variants.

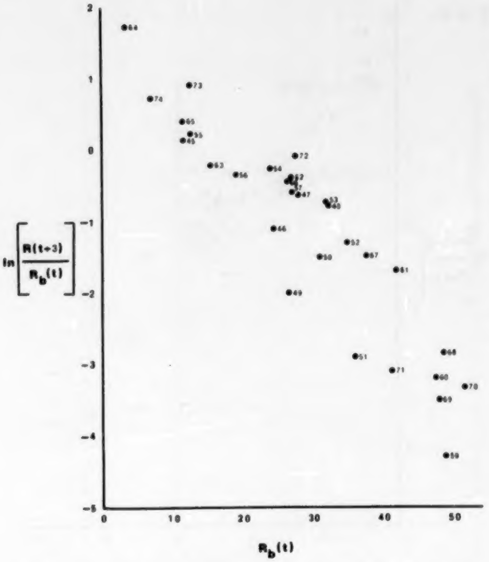

FIG. 13. Year-labeled linear transformation of Ricker model (B1) relating extracted year-class strength estimates (R) to estimated parent stock egg capacity (R_b). Based on extracted year-class strength estimates assuming that exploitation and survival rates for vulnerable males are constant ($E = 0.85$, $S = 0.10$), an annual unexploited survival rate of 0.80, and that 20% of females breed at age 2.

of k_0 correspond to regions of stable cycling with 7-yr period in the exploited case, and with 9-yr period in the unexploited case (Table 5).

Regression analyses thus seem to complement and reinforce modeling conclusions. Strong statistical relations between variables derived from landings and effort data were obtained only at a 3-yr lag, indicating negligible statistical impact of possible density-dependent mechanisms beyond the settling stage on year-class strength. The age-structured Ricker curve, model B1′, "fit" generated data very well, and considerably better than did the mixed model B3′. We observe that for model B1′, year-class strength at age 2 depends only on a weighted average of adult female densities 3 yr previous.

Model Predictions

We now have settled on a particular model variant, with specific biological assumptions incorporated into its form and parameter values. We do not claim that this model represents reality, only that it is consistent with the evidence so far available. By manipulating the model further, we will be able to determine its behavior under new circumstances and thereby generate testable hypotheses about the real biological system.

TABLE 5. Linear regression analysis results for the "mixed" model, B3′. The estimates of k_0 have been adjusted to a normalized equilibrium year-class strength of one by: $k_0^* = k_0 \times (X_0/1)$, where X_0 = equilibrium year-class strength at age 2 based on estimated parameters, m and k_0.

	Estimates				
Model assumptions	m	k_0	k_0^*	X_0	R^2
Constant exploitation and survival rates					
20% females breed age 2:					
Food competition	6.47	0.132	1.089	8.25	0.757
Random encounters	4.04	0.151	1.223	8.10	0.598
100% females breed age 2:					
Food competition	4.83	0.128	1.038	8.11	0.779
Random encounters	3.25	0.150	1.193	7.95	0.647
Variable exploitation and survival rates					
20% females breed age 2:					
Food competition	5.59	0.093	1.035	11.13	0.616
Random encounters	4.65	0.114	1.293	11.34	0.565
100% females breed age 2:					
Food competition	4.37	0.091	1.000	10.99	0.657
Random encounters	3.85	0.114	1.277	11.20	0.626

In this section we undertake two numerical experiments to probe the model. The first of these is quite straightforward: The model is "run" to produce a simulation of the past record of the fishery — annual landings and initial stock abundance. The results, displayed in Fig. 14, should be compared directly with the (more) empirical graph in Fig. 2. The correspondence seems quite satisfactory, although agreement is imperfect.

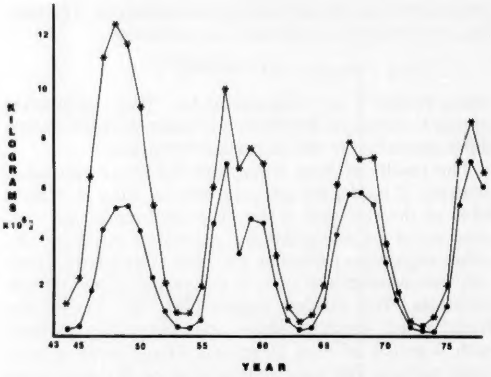

FIG. 14. Simulated initial harvestable abundance (upper line) and fishery landings (lower line) of Dungeness crab in the Northern California fishery, 1943–78. Simulation employs specific parameter values for ℓ and k ($\ell = 0.96$, $k = 0$) to generate year-class strength. Landings and initial abundance employ estimated (variable) existing exploitation and survival rates for vulnerable males in appropriate years.

The second numerical experiment is to undertake a (simulated) female harvest. We find that the effect of female harvest is, for the model, to increase stock levels and to damp down the periodic oscillations of population. The degree to which these things occur depends rather sensitively on model parameters, so that a real experiment in female harvesting, were it feasible, would provide substantial refinement of the model (and presumably an enhanced understanding of the real biological system).

The remainder of this section is devoted to analysis of a simple management strategy for female harvest, and the simulated results of its application.

Our adopted model is of the form

$$\begin{aligned} R(t) &= mR_b(t-3)\,e^{-\ell R_b(t-3)}. \\ &= G[R_b(t-3)]. \end{aligned}$$

It is quite easy to incorporate any proportional female harvest policy into this model, by setting

$$\begin{aligned} R_b(t) = {} & B_0S_0(t)R(t) + B_1S_1(t)S_0(t-1)R(t-1) \\ & + B_2S_2(t)S_1(t-1)S_0(t-2)R(t-2) \\ & + B_3S_3(t)S_2(t-1)S_1(t-2)S_0(t-3)R(t-3) \end{aligned}$$

Assuming that harvest is applied directly before breeding, $S_k(t)$ is the fraction of the k-th age-class females which escape the fishery in year t. Equivalently, $S_k(t)$ gives the fraction of the k-th age-class females allowed to breed at t. Thus, $0 < S_k(t) \leq 1$.

The steady-state equilibrium of the model has

$$S_k(t) \equiv S_k^* \quad \text{and} \quad R(t) \equiv R^*,$$

independent of t. Thus with

$$\begin{aligned} B^* = {} & B_0S_0^* + B_1S_0^*S_1^* + B_2S_0^*S_1^*S_2^* \\ & + B_3S_0^*S_1^*S_2^*S_3^* \end{aligned}$$

and

$$R_b^* = B^*R^*,$$

the equilibrium equation is

$$R^* = G(R_b^*) \quad \text{or equivalently} \quad R_b^* = B^*G(R_b^*).$$

Notice that $0 < B^* \leq B$, with B the nonharvest natality multiplier.

Let us now specify our goal to be adjusting harvest level, and hence B^*, so as to maximize R^* at a level R^m. Differentiating the equilibrium equation $R^* = G(B^*R^*)$ implicitly by B^*, we see that the maximum R^m occurs for the values B^m and $R_b^m = B^mR^m$ which satisfy the pair of equations

$$R_b^m = B^mG(R_b^m), \quad 0 = G'(R_b^m).$$

Recalling that $B^m \leq B$, we see (Fig. 15) this requires that the equilibrium level R_b which prevails in the absence of a female harvest must lie under the descending branch of the G curve — a condition which is met by our Dungeness crab model.

Solving the pair of equations explicitly when G is the Ricker curve yields

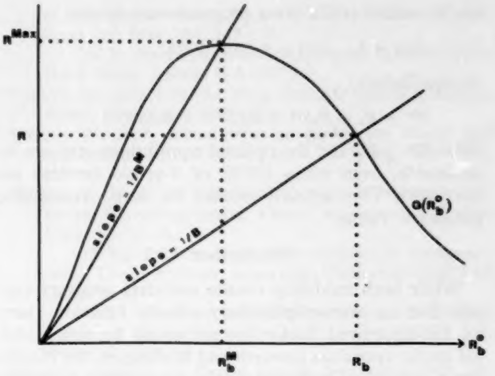

FIG. 15. Maximizing year-class strength through optimal female harvest.

$$B^m = e/m, \quad R_b^m = 1/\ell, \quad \text{and hence} \quad R^m = m/\ell e.$$

It remains to relate B^m to the optimal proportional harvest policy, i.e., the specification of $S_0{}^m$, $S_1{}^m$, $S_2{}^m$, and $S_3{}^m$. Here there are many possibilities, but we shall consider only two:

1) All age-groups 2–5 are harvested at the same proportionate levels:

$$S_0(t) = S_1(t) = S_2(t) = S_3(t). \text{ At equilibrium}$$

$$B^m = B_0S^m + B_1(S^m)^2 + B_2(S^m)^3 + B_3(S^m)^4,$$

so that the optimal equilibrium level is always attainable by a certain (unique) escapement level S^m. In Table 6 we see the results for several choices of the model's parameters. Note that optimal harvest intensity and resulting year-class strength depend sensitively on the model parameters.

2) Age 2 females are not harvested; age 3–5 females

TABLE 6. Maximum equilibrium year-class strength at age 2 (R^M), Ricker curve parameter (ℓ), and optimal female escapement fraction (S^M) when female crabs may be harvested from ages 2 through 5. R^M is espressed in normalized units.

ℓ	R^M	S^M
0.32	1.00	≐1
0.48	1.07	0.86
0.64	1.30	0.73
0.80	1.67	0.60
0.96	2.23	0.50
1.12	3.08	0.40
1.28	4.33	0.32

are harvested at the same proportionate level:

$$S_0(t) \equiv 1, \quad S_1(t) = S_2(t) = S_3(t).$$

At equilibrium:

$$B^m = B_0 + B_1S^m + B_2(S^m)^2 + B_3(S^m)^3.$$

Thus $B^m \geq B_0$ and the optimal equilibrium may not be attainable, even when 100% of 3-yr-old females are harvested. This actually occurs for some reasonable parameter values.

Discussion

While both modeling results and data analyses suggest that an overcompensatory natality function (here an age-structured Ricker curve) could be responsible for cyclic year-class strength and landings in the Northern California Dungeness crab population, we would certainly not immediately infer that such a biological control mechanism is indeed responsible. Available data are not sufficient to entirely exclude the possibility that crab cycles are exogenously determined. Ours is a "conditional" analysis whose initial premise is a presumption of biological control. At the same time, however, we feel little hesitation in concluding that neither Beverton-Holt natality nor intense juvenile cannibalism are likely significant factors in Dungeness crab dynamics. The primary value of the modeling and data analysis process in this case has been to allow rejection of biological control mechanisms which are "a priori" plausible, but which clearly fail to pass diagnostic tests.

If one accepts the essential validity of the diagnostic tests, the combination of model evaluation and statistical support for modeling contentions seems remarkably effective and consistent. The diagnostic tests themselves, however, may be legitimately criticized and, in general, diagnostic tests may not be available which might allow the process of elimination approach employed in this study.

Diagnostic tests relied on period, amplitude, and time series pattern of landings and of extracted estimates of year-class strength. This pattern, regardless of manipulation, suggests moderately regular cyclic fluctuations, not chaotic in nature. The most reasonable estimate of period is 9–10 yr, but this estimate assumes constant period length and is based on a data set including less than four complete cycles. Modeling showed that period length is not necessarily an integer value and thus one would not expect annual landings data to repeat in an exact periodic pattern even if cycles were perfect and without noise. Clearly, had the Dungeness time series not exhibited substantial, regular fluctuations, diagnostic tests would not have been possible. Modeling showed that any of the plausible alternatives could exhibit stable population behavior with the desired equilibrium levels, simply by suitable choice of parameters.

Modeling confirmed that stable cycling is a regular property of age-structured overcompensatory natality functions such as the Ricker curve. It must be remembered, however, that these are cycles in year-class strength. Cycles in year-class strength, should they exist in a population, need not be reflected in gross landings from a fishery. In the Dungeness fishery, one sees cycles in landings largely because of rather intense exploitation and because only a few age-classes are represented in landings. The age composition of landings is often dominated by the age-class just entering the fishery and currently seems never to include more than three age-classes. In fisheries which have generally lower exploitation rates and which are based on long-lived species, amplitude of fluctuations in year-class strength would have to be extremely large and have a period sufficiently long to prevent masking of possibly cyclic fluctuations in year-class strength by gross landings measures. Accurate extraction of year-class strength from landings figures requires information concerning age-composition, weight at age, survival rates, gear selection, and fishing effort. This information is rarely available. Were it all available for Dungeness crab, the admittedly crude extraction techniques employed in this study could be greatly improved.

Since fishery landings reflect contributions from many age-classes and depend on fishing effort, we feel it is premature to conclude that the Northern California population exhibits an unstable regime and is destined for a crash. As shown in this paper, crude but justifiable adjustments of landings data for fluctuations in fishing effort fail to show the apparent increase in amplitude seen in unadjusted landings (Fig. 2). Of the two model variants which were most plausible, only the mixed model suggested that exploitation should increase amplitude of fluctuations. This model, however, exhibited what we feel to be an unacceptable period depression and would require exploited periods of about 7 yr. The more plausible Ricker natality model suggests no change in period or amplitude due to exclusive harvest of males.

The Ricker natality model suggests that year-class strength is determined by the age of settlement and this suggests that study of survival from egg to settling should have high priority. Such study, whether it focuses on larval metamorphosis, predation by nemertean worms, or whatever, of necessity requires information adequate to allow reliable estimation of the annual egg capacity of the Dungeness population. Such estimates require basic information concerning the female stock of Dungeness in Northern California — age and growth, fecundity, survival rates, stock age composition. Lack of fundamental knowledge of the female component of any population would seem to be indefensible if it is desired to seriously and objectively evaluate alternative hypotheses involving biological control. Until such information exists, and unless collected information conforms to general study modeling and data analyses, we are not advocating female harvest. We note, however, that extracted estimates of female egg capacity and resulting year-class strength clearly shows that largest year-classes are not produced by largest female stock sizes. Additionally, we feel the general controversy surrounding female harvest could well profit from comparative studies of crab fisheries which are managed for both male and female harvest (e.g. the European fishery for *Cancer pagurus.*)

Hypotheses regarding Dungeness dynamics seem to have been based either on exogenous (the upwelling hypothesis) or endogenous (compensatory feedback) control mechanisms. It is not unlikely that both endogenous and exogenous factors influence Dungeness recruitment and perhaps each in a significant way. It might be interesting to investigate model population behavior which depends on both internal and external controls, in this case compensatory biological feedback and upwelling. It would be important, however, that time-lags appropriate to each of the possible controls be carefully considered and that they be biologically plausible. That we chose an initial presumption of endogenous control does of course reflect our current bias. This bias does not ignore the striking visual relation between upwelling and crab landings. Rather, it questions the biological plausibility of a time-lag of less than 2 yr between upwelling and crab landings. It seems unlikely that upwelling would exert its potentially important effects upon those crab life-stages presumably least sensitive to exogenous variations.

Acknowledgments

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Appendix I

We begin with the renewal equation from section 3.

$$R(t) = G[R_b(t-3)] \prod_{k=1}^{3} F_{3-k}[R_d(t-k)]$$

where

$$R_b(t) = \sum_{j=0}^{3} B_j R(t-j), \quad R_d(t) = \sum_{j=0}^{3} D_j R(t-j),$$

and with the equilibrium solution, $R^* \equiv$ constant, which satisfies

$$R^* = G(BR^*) \prod_{k=1}^{3} F_{3-k}(DR^*); \; B = \sum_{j=0}^{3} B_j, \; D = \sum_{j=0}^{3} D_j.$$

Let us examine small displacements $r(t) = R(t) - R^*$ of a varying population $R(t)$ from equilibrium. Setting

$$(\alpha 1) \quad r_b(t) = R_b(t) - BR^* = \sum_{j=0}^{3} B_j r_j(t-j)$$

and

$$(\alpha 2) \quad r_d(t) = R_d(t) - DR^* = \sum_{j=0}^{3} D_j r_j(t-j),$$

these being the displacements from equilibrium of the effective compensatory maternal and general adult populations, one finds for $r(t)$ the exact dynamic equation

$$(\alpha 3) \quad r(t) = G[r_b(t-3) + BR^*] \prod_{k=1}^{3} F_{3-k}[r_d(t-k) + DR^*].$$

Expanding the factors on the right in Taylor series about equilibrium

$$G[r_b + BR^*] = G(BR^*) + G'(BR^*) \cdot r_b + \ldots,$$

$$F[r_d + DR^*] = F(DR^*) + F'(DR^*) \cdot r_d + \ldots,$$

multiplying out the product, and substituting from the equilibrium equation yields

$$\frac{r(t)}{R^*} = \frac{G'(BR^*)}{G(BR^*)} r_b(t-3) + \sum_{k=1}^{3} \frac{F'_{3-k}(DR^*)}{F_{3-k}(DR^*)} r_d(t-k) + \ldots$$

The missing terms, indicated by three dots, all are of quadratic or higher order in r_b and r_d. Assuming small displacements $r(t)$, and hence small $r_b(t)$ and $r_d(t)$, one justifies dropping these higher order terms to arrive at the linear variational approximation of section 4:

$$(\alpha 4) \quad v(t) = \eta_b v_b(t-3) + \sum_{k=1}^{3} \eta d_{3-k} v_d(t-k),$$

where

$$(\alpha 5) \quad v_b(t) = \sum_{j=0}^{3} B_j v(t-j), \quad v_d(t) = \sum_{j=0}^{3} D_j v(t-j).$$

If the system (α1–α3) is combined into a single equation, one has a single sixth order nonlinear difference equation for r, of the form

$$r(t) = f[r(t-1), r(t-2), \ldots, r(t-6)]$$

Similarly, if the system (α4–α5) is combined into a single equation, it is a sixth order linear difference equation of the form

$$(\alpha 6) \quad v(t) = \sum_{k=1}^{6} a_k v(t-k);$$

this equation has been written more explicitly in section 4.

It is thus clear that a full description of the present state of the dynamic system, adequate to determine its future evolution, requires specification of a six-component phase vector

$$\mathbf{r}(t) = [r(t), r(t-1), r(t-2), \ldots, r(t-5)]^T$$

(Equivalently, one could specify the present population numbers of the six age-groups $N_0(t), N_1(t), \ldots, N_5(t)$.)

The evolution of the variational vector

$$\mathbf{v}(t) = [v(t), v(t-1), v(t-2), \ldots, v(t-5)]^T$$

is governed by the matrix difference equation $\mathbf{v}(t) = A\mathbf{v}(t-1)$ where A is the six by six matrix (see α6)

$$A = \begin{bmatrix} a_1 & a_2 & a_3 & a_4 & a_5 & a_6 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix}$$

This resembles the usual Leslie population matrix; however, the entries a_j may be negative instead of always ≥ 0.

The eigenvalues of A satisfy the characteristic equation of section 4: $\phi(\lambda) = 0$ where

$$(\alpha 7) \quad \phi(\lambda) = \lambda^6 - \sum_{k=1}^{6} a_k \lambda^{6-k}$$

Suppose that the characteristic equation has a conjugate pair of simple roots $\lambda_\pm = r[\cos\theta \pm i \sin\theta]$ with $r > 1$ and that all other roots have modulus <1. Then there exists a two-dimensional linear subspace L_0 of the six-dimensional phase space which in the linearized problem $\mathbf{v}(t) = A\mathbf{v}(t-1)$ is invariant and attracting. L_0 is, namely, the span of the eigenvectors of A corresponding to eigenvalues λ_+ and λ_-. Any orbit of the linearized equation tends asymptotically to the plane L_0; any orbit initially in L_0 stays there. The orbits in L_0 are unstable and diverge to infinity. For the full nonlinear problem, L_0 is replaced by an invariant manifold L, which is a two-dimensional curved surface, tangent to L_0 at the origin (equilibrium point). The orbits $\mathbf{r}(t)$ of the nonlinear problem *are* stable: they approach a closed cycle lying in L. Our idea is to project these orbits onto L_0, so as to appraise their period, amplitude, and waveform.

Let λ be any eigenvalue of A. One may verify directly the form of the corresponding eigenvector $\mathbf{v}_\lambda$ (satisfies $A\mathbf{v}_\lambda = \lambda\mathbf{v}_\lambda$) and eigenvector $\mathbf{w}_\lambda$ (satisfies $A^T\mathbf{w}_\lambda = \lambda\mathbf{w}_\lambda$). Namely,

$$\mathbf{v}_\lambda = \begin{bmatrix} \lambda^5 \\ \lambda^4 \\ \cdot \\ \cdot \\ \cdot \\ \lambda \\ 1 \end{bmatrix} \quad \text{and} \quad \mathbf{w}_\lambda = \begin{bmatrix} 1 \\ \lambda - a_1 \\ \lambda^2 - (a_1\lambda + a_2) \\ \cdot \\ \cdot \\ \cdot \\ \lambda^5 - (a_1\lambda^4 + \ldots + a_5) \end{bmatrix}$$

These form a biorthogonal set with respect to the inner product

$$[\mathbf{v}, \mathbf{w}] = \sum_{n=1}^{6} v_n w_n.$$ That is, $[\mathbf{v}_\lambda, \mathbf{w}_\mu] = 0$ when $\mu \neq \lambda$ and

$$[\mathbf{v}_\lambda, \mathbf{w}_\lambda] = \phi'(\lambda).$$

($\phi'(\lambda) \neq 0$ at an eigenvalue λ which is a simple root of the characteristic equation $\phi(\lambda) = 0$.)

Now consider a complex conjugate pair of simple eigenvalues $\lambda_\pm = r[\cos\theta \pm i \sin\theta]$. For brevity put $\mathbf{v}_{\lambda\pm} = \mathbf{v}_\pm$, $\mathbf{w}_{\lambda\pm} = \mathbf{w}_\pm$, $\phi'(\lambda_\pm) = \phi_\pm$, and note that $\mathbf{v}_- = \bar{\mathbf{v}}_+$, $\mathbf{w}_- = \bar{\mathbf{w}}_+$ and $\phi_- = \bar{\phi}_+$. (The bar over denotes complex conjugate). From biorthogonality

$$[\mathbf{v}_+, \mathbf{w}_-] = [\mathbf{v}_-, \mathbf{w}_+] = 0, \quad [\mathbf{v}_+, \mathbf{w}_+] = \phi_+, \quad [\mathbf{v}_-, \mathbf{w}_-] = \phi_-.$$

The projection $P\mathbf{y}$ of any vector $\mathbf{y}$ onto the two-dimensional eigenspace spanned by $\mathbf{v}_+$ and $\mathbf{v}_-$ is $P\mathbf{y} = c_+\mathbf{v}_+ + c_-\mathbf{v}_-$, where

$$c_+ = [\mathbf{y}, \mathbf{w}_+]/\phi_+ \quad \text{and} \quad c_- = [\mathbf{y}, \mathbf{w}_-]/\phi_-.$$

It is this eigenspace which will be tangent to the two-dimensional stable manifold for the nonlinear dynamics.

It is expedient to rewrite this expression for $P\mathbf{y}$ in terms of vectors with real components. Introduce

$$\mathbf{v}_c = Re\,\mathbf{v}_\pm = \begin{bmatrix} r^5 \cos 5\theta \\ r^4 \cos 4\theta \\ \cdot \\ \cdot \\ \cdot \\ r\cos\theta \\ 1 \end{bmatrix}, \quad \mathbf{v}_s = \pm Im\,\mathbf{v}_\pm = \begin{bmatrix} r^5 \sin 5\theta \\ r^4 \sin 4\theta \\ \cdot \\ \cdot \\ \cdot \\ r\sin\theta \\ 0 \end{bmatrix},$$

and similarly

$$\mathbf{w}_c = Re\,\mathbf{w}_\pm, \quad \mathbf{w}_s = \pm Im\,\mathbf{w}_\pm; \quad \phi_c = Re\,\phi_\pm, \quad \phi_s = \pm Im\,\phi_\pm.$$

then

$$P\mathbf{y} = c_c\mathbf{v}_c + c_s\mathbf{v}_s, \quad \text{where} \quad c_c = \frac{2[\mathbf{y}, \mathbf{w}_c]\phi_c + 2[\mathbf{y}, \mathbf{w}_s]\phi_s}{\phi_c^2 + \phi_s^2}$$

and

$$c_s = \frac{2[\mathbf{y}, \mathbf{w}_c]\phi_s - 2[\mathbf{y}, \mathbf{w}_s]\phi_c}{\phi_c^2 + \phi_s^2}.$$

A final step is to orthonormalize $\mathbf{v}_c$ and $\mathbf{v}_s$ by means of the Schmidt process.

NOTES

Comparison of Two Methods of Estimating the Variance of the Estimate of Catch Per Unit Effort

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Smith, S. J. 1980. Comparison of two methods of estimating the variance of the estimate of catch per unit effort. Can. J. Fish. Aquat. Sci. 37: 2346–2351.

Two methods of estimating the variance of the estimate of catch per unit effort are compared empirically here. The second method, an application of the Jackknife estimator proved to be the overall best technique due to its generality. In addition the Jackknife method provides means for the estimation of confidence intervals.

Key words: catch per unit effort, variance estimation, Jackknife estimator

Smith, S. J. 1980. Comparison of two methods of estimating the variance of the estimate of catch per unit effort. Can. J. Fish. Aquat. Sci. 37: 2346–2351.

La note qui suit offre une comparaison empirique de deux méthodes de calcul de la variance de l'estimation des prises par unité d'effort. La seconde méthode, une application de l'estimateur « Jackknife », s'est avérée la meilleure des deux à cause de sa généralité. En outre, elle permetd'estimer les intervalles de confiance.

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Catch per unit effort where the effort is defined here with respect to days or hours spent fishing for a specific species with a standard gear is one index of abundance used in fisheries work (Royce 1972). For this statistic to be used in a comparative sense, say month-to-month or year-to-year comparisons, an estimate of the variance of the statistic is needed.

Two methods of estimating this variance are investigated empirically here. The first method, a regression technique, requires specific assumptions to be met in order to be valid. The second method is an application of the so called "Jackknife" estimator and is more general in its use.

Both methods are applied to commercial data on yellowtail flounder (*Limanda ferruginea*) and American plaice (*Hippoglossoides platessoides*) catches by Newfoundland vessels (stern trawlers 501–900 GRT used as the standard) for the Grand Bank area (ICNAF Div. 3LNO) in the year 1976, 1977, and 1978.

Notation

Define

$K_i =$ the number of trip components reported for the ith month,

$L =$ the number of trip components reported for the year,

$f_{ij} =$ the effort expended for the standard gear measured by the number of days (hours) . . . . . $i = 1, 2, \ldots, 12$.

$C_{ij} =$ the catch (kg) of the jth trip component in the ith month.

The term "trip component" is defined here with respect to its use at the Northwest Atlantic Fisheries Centre. The data summarized from the original fishing logs, is categorized according to the ICNAF/NAFO Division being fished, unit area being fished, depth, and main species. It is conceivable that in any one trip a vessel may fish in many different divisions, unit area, etc., with each day's fishing results entered in the log for the trip. When summarizing the results of this trip for data processing, all fishing entries in the same division, unit area, and depth zone for the same main species are combined as one entry; hence these records are terms "trip components."

In general, the trip components can be defined by any reasonable criteria as long as there is continuity of space, time, and species. Catch per unit effort is calculated by;

$$(1) \quad C_i/f_i = \frac{\sum_{j=1}^{K_i} C_{ij}}{\sum_{j=1}^{K_i} f_{ij}},$$

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for the month and

$$(2)\quad C/f = \frac{\sum_{i=1}^{12}\sum_{j=1}^{K_i} C_{ij}}{\sum_{i=1}^{12}\sum_{j=1}^{K_i} f_{ij}},$$

for the year. The time periods (year, month) used in the above are intended only for example. In actuality time periods would have to be defined so that assumptions dealing with seasonal trends in catchability would be taken into account.

The estimators as defined in (1) and (2) are in the class of ratio estimators since both the C_{ij} and the f_{ij} are random variables. In general estimators of this class are biased estimators with bias of order $1/n$, where n is the sample size (Cochran 1977). In general sample sizes tend to be quite large for catch effort data, so that the bias is extremely small. Although the methods studied in this paper are being considered from a variance estimation point of view, these techniques also provide means by which the bias can be reduced or eliminated altogether (given certain conditions are met).

The Estimators

Regression technique — A well known result from regression states that if a linear relationship of the form,

$$(3)\quad C = \beta f + \epsilon,$$

holds then $\sum W \cdot Cf / \sum W \cdot f^2$ is an unbiased estimator of the population ratio β, where W is defined as a weight in the sense of a weighted least squares (Snedecor and Cochran 1967; Cochran 1977). The weight, W, would be equal to 1, $1/f$, or $1/f^2$ according to whether the variance of C was constant with respect to f, proportional to f or proportional to f^2, respectively. Given one of these three conditions then, the estimator of β would be one of,

$$(4)\quad T_1 = \frac{\sum Cf}{\sum f^2},$$

$$(5)\quad T_2 = \frac{\sum C}{\sum f},$$

or,

$$(6)\quad T_3 = \frac{\sum C/f}{n},$$

where n in this case would be either K_i or L depending upon whether it was the monthly or yearly estimates we are interested in. The estimator T_1 is the usual least squares estimators, T_2 is identical to the estimators in (1) and (2) and T_3 is a form of a grand mean of individual trip components ratios.

The first step in using this technique is to fit a model of the form

$$(7)\quad C = \alpha + \beta f + \epsilon,$$

and then determine if the line passes through the origin by testing the null hypothesis, H_0: $\alpha = 0$ versus the alternative, H_a: $\alpha \neq 0$ by the usual procedures. If the null hypothesis of zero intercept can not be rejected, that is (3) is the appropriate model, then a plot of the residuals $(C - \hat{C})$ against the values of f would indicate the appropriate value of W to use.

The estimate of the variance of β would then be of the form (Draper and Smith 1966),

$$(8)\quad \widehat{\mathrm{Var}(\beta)} = \frac{\dfrac{\sum W \cdot (C - \hat{C})^2}{n-1}}{\sum W \cdot f^2}.$$

One limitation of this method, given all assumptions are valid, is that a minimum of three observations are required in order that there will be at least one degree of freedom available for the testing of hypotheses.

The Jackknife technique — The Jackknife was originally developed by Quenouille (1949) as a means of reducing bias of a serial correlation estimator. The name "Jackknife" was coined by John Tukey in an unpublished work. A recent review of the technique has been made by Miller (1974).

Let $Y_1, \ldots, Y_n$ be a sample of independent and identically distributed random variables. Also let $\hat{\theta}$ be an estimator of the population parameter θ based on the sample of n observations. Further define θ_{-i} to be the corresponding estimator based on all the sample points, excluding the ith point.

The estimator

$$(9)\quad \theta_J = n\theta - (n-1) \cdot \frac{1}{n} \sum_{i=1}^{n} \theta_{-i}$$

known generally as the first order Jackknife estimator has the property of eliminating bias of the order $1/n$ (Miller 1974).

Durbin (1959) presented results in a note demonstrating that, for the class of ratio estimators where there existed a linear relationship between the numerator and the denominator, not only did the use of the Jackknife reduce the bias but it also reduced the variance. These results were specific for cases when the denominator had a normal distribution.

The Jackknife estimator used here, denoted by R_J is the average of the n quantities (K_i for the month, L quantities for year),

$$(10)\quad R_{-j}' = n \cdot C/f - (n-1) R_{-j},$$

where $R_{-j} = \sum C_{ij} / \sum f_{ij}$, with the jth observation removed. The estimate of the variance of R_J, $\widehat{V(R_J)}$ would be

$$(11)\quad \widehat{V(R_J)} = \frac{1}{n(n-1)} \sum^{n} (R_{-j}' - R_J)^2$$

The variance estimator in (11) is an asymptotically unbiased estimator (Cochran 1977).

Further it has been postulated by Tukey (1958) that if the n values (10) can be treated as approximately independent and identically distributed random variables, the statistic

$$(12)\quad \frac{R_J - R}{(\widehat{V(R_J)})^{1/2}}$$

should have an approximate Student's-t distribution with $n-1$ degrees of freedom. This postulate, if valid, would provide the means for interval estimation and hypothesis testing.

The variance estimation aspect of the Jackknife methods has been successfully exploited in many applications, especially in

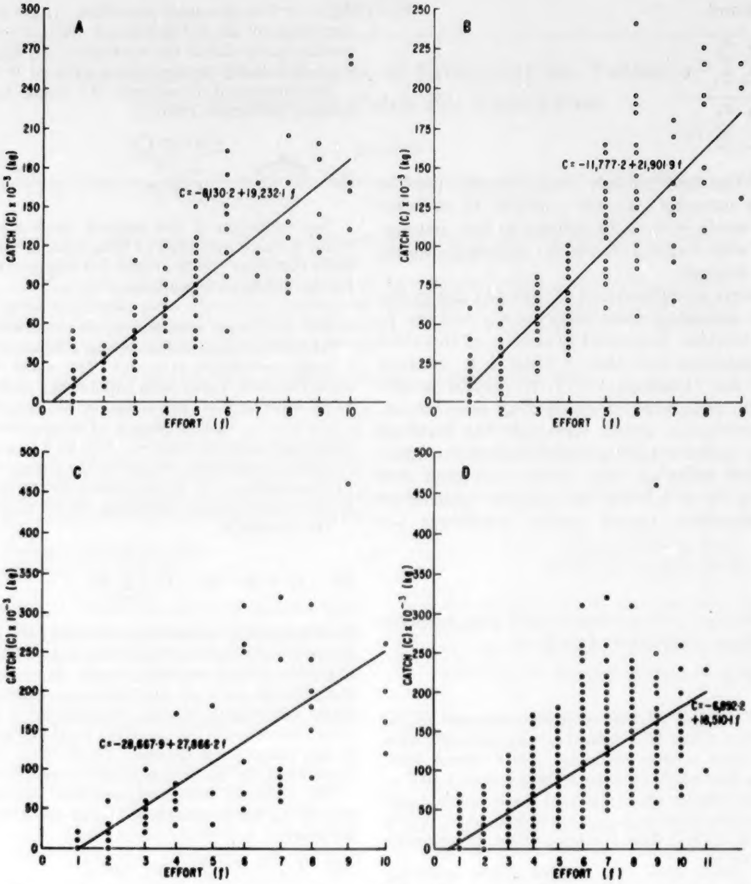

FIG. 1. Catch vs. effort for American plaice, with fitted line (A, July; B, August; C, December; D, year [1978]).

situations where nonlinear estimates are involved (as is the case here). Some examples of this are Manly (1977) (mark–recapture estimators), Zahl (1977) (indices of diversity) and Gladen (1979) (toxicological effects).

A limitation of the Jackknife technique is the need for at least two observations before calculation can be made.

Results

The methods for estimating were applied to commercial fishing data collected from Newfoundland vessels.

The regression method presented itself to be an extremely lengthy form of analysis and therefore was applied to 1978 data only. The process required fitting the model in (7) to the data for each month and the year as a whole. Hypothesis tests were performed and residual plots were examined for each regression. Based on the patterns of the residuals an appropriate weight was chosen and the model in (3) was then fitted to the data.

Intuitively one would expect that the regression of catch on effort would pass through the origin after all no effort should result in a zero catch. This did not always occur. The scatter diagrams for cases of nonzero intercepts for American plaice and yellowtail flounder are depicted in Fig. 1 and 2, respectively. Increasing variability of catches with respect to an increase in effort resulted in negative intercepts for the plaice regressions while just the reverse held true for the yellowtail.

The trend of increasing variance with the increase in effort was also evident in the residual plots on the

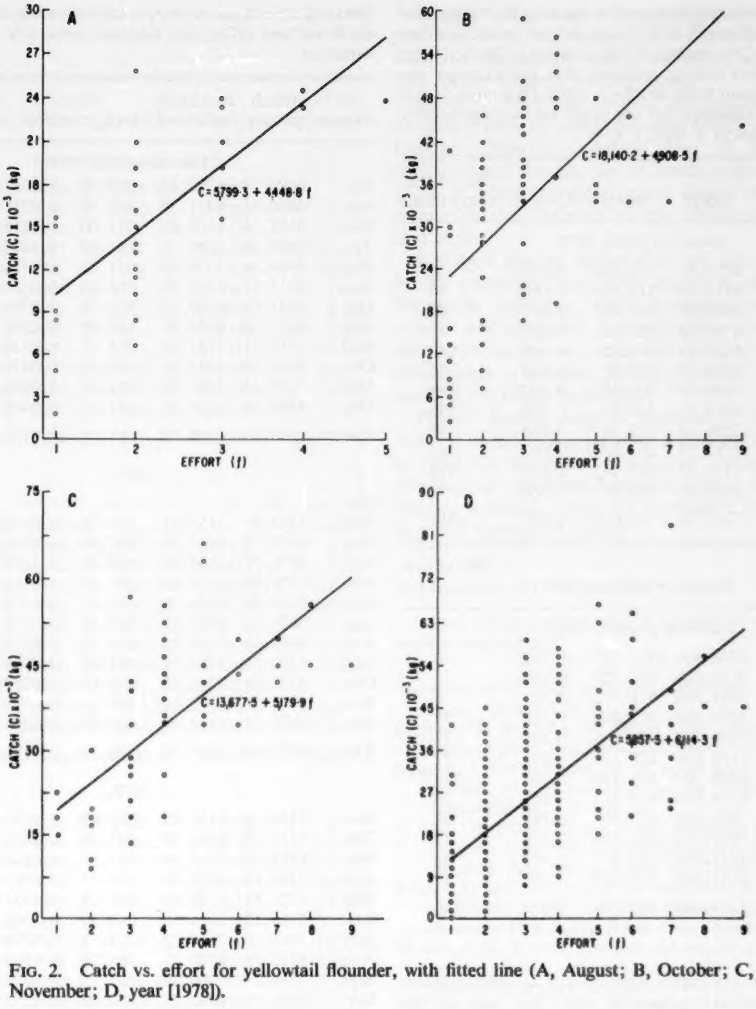

FIG. 2. Catch vs. effort for yellowtail flounder, with fitted line (A, August; B, October; C, November; D, year [1978]).

plaice regressions, thus suggesting a weight of $1/f_{ij}$. Therefore the estimator T_2 was used for the American plaice and these results are presented in Table 1.

The small sample sizes for the yellowtail flounder data reduced the interpretative value of the residual plots. The residual plot for the year as a whole indicated that the variance of the catch was constant with respect to the value of f_{ij}. The estimator T_1 was deemed suitable for the individual months data on the basis of the years' residual plots. Doing this, of course ignores any effects of seasonal trends, the consequences of which will be discussed later.

The Jackknife technique was applied to of data for 1976, 1977, and 1978. With respect to computation and analysis time, this method was far more efficient than the regression method. The results for plaice and yellowtail are listed in Table 2 and 3, respectively.

As a preliminary step frequency diagrams of the values as defined in (10) were examined to determine if approximate confidence intervals can be constructed using a Students-t distribution. The individual plots are not presented because most of the histograms were symmetrical in form. Generally the symmetry was definite for sample sizes greater than 92 for the American plaice. Individual month results for yellowtail flounder were difficult to assess due to small sample sizes (less

TABLE 1. Regression technique of estimating the variance of catch per unit effort (T_1 and T_2 are defined in the text. SE: standard error, CV: coefficient of variation). (Note: [1] an asterisk in the first column indicates that the intercept was significantly different from zero [$\alpha = 0.05$]; [2] a cross (+) in the first column indicates that the slope was not significantly different from zero [$\alpha = 0.05$].)

Month	T_2(kg)	SE(T_2)	CV(T_2)	No. of trip components
American plaice 1978				
Jan.	6150.78	339.259	0.055	65
Feb.	6175.59	515.449	0.083	44
Mar.	6418.45	543.937	0.085	45
Apr.	4298.22	299.92	0.069	71
May	6221.85	264.88	0.043	123
June	6914.27	195.87	0.028	186
July* (0.011)	7666.10	206.93	0.027	185
Aug.* (0.001)	8372.73	238.93	0.029	195
Sept.	7896.75	272.78	0.035	156
Oct.	8292.34	275.83	0.033	161
Nov.	7128.69	295.75	0.041	118
Dec.* (0.011)	9353.04	602.99	0.064	92
Year* (<0.001)	7453.76	93.048	0.013	1441

Month	T_1(kg)	SE(T_1)	CV(T_1)	No. of trip components
Yellowtail flounder 1978				
Jan.	8948.461	1372.783	0.153	6
Feb. +	4786.656	981.320	0.205	3
Mar.	7881.992	918.312	0.117	6
Apr.	5863.395	513.669	0.088	38
May	6166.504	474.649	0.077	33
June	5118.836	229.340	0.045	32
July	6448.164	651.116	0.101	19
Aug.* (0.011)	6646.086	412.137	0.062	28
Sept.	7604.953	675.269	0.089	41
Oct.* (<0.001)	9969.473	553.544	0.056	73
Nov.* (<0.001)	7857.199	375.341	0.048	53
Dec.	8291.691	867.205	0.105	14
Year* (<0.001)	7714.484	195.078	0.025	346

than 70). Therefore, since these results are preliminary, confidence intervals estimated with the use of the pivotal value defined in (12) can be constructed, but will probably be more accurate near the center of the distribution than in the tails.

Discussion and Conclusions

If the better estimator is defined as the one which has the smallest coefficient of variation, then the regression estimators were consistently better for the 1978 data, albeit the differences in many cases were minimal.

TABLE 2. Jackknife technique of estimating the variance of catch per unit effort (SE: standard error, CV: coefficient of variation).

Month	Catch per day	Jackknife estimates	SE(R_J)	CV(R_J)	No. of trip components
American plaice 1976					
Jan.	6695.77	6700.32	259.38	0.0387	158
Feb.	6436.45	6441.10	342.38	0.0532	107
Mar.	6585.74	6609.85	751.00	0.1136	95
Apr.	6864.20	6888.74	1014.64	0.1473	61
May	5066.14	5069.08	241.23	0.0476	100
June	6215.57	6218.49	201.47	0.0324	192
July	6345.64	6349.52	192.04	0.0302	189
Aug.	6945.10	6948.81	183.88	0.0265	148
Sept.	7319.11	7323.75	266.81	0.0310	266
Oct.	6405.16	6412.03	288.35	0.0450	186
Nov.	5427.62	5430.08	161.98	0.0298	136
Dec.	6198.29	6203.33	251.60	0.0406	76
Year	6393.63	6396.12	81.05	0.0127	1714
1977					
Jan.	—	—	—	—	—
Feb.	7145.87	7153.31	535.51	0.0749	107
Mar.	4397.75	4414.39	437.90	0.0992	37
Apr.	4876.79	4898.87	542.43	0.1107	28
May	6708.60	6715.02	271.29	0.0404	84
June	6950.88	6954.30	193.63	0.0278	173
July	6638.65	6641.87	224.27	0.0338	168
Aug.	6493.39	6494.05	179.53	0.0276	202
Sept.	6289.41	6292.21	193.60	0.0308	226
Oct.	5253.83	5255.62	148.67	0.0283	258
Nov.	6734.71	6738.42	220.34	0.0327	171
Dec.	6827.21	6832.44	306.00	0.0448	150
Year	6416.47	6417.51	76.19	0.0119	1604
1978					
Jan.	6150.78	6155.85	362.83	0.0589	65
Feb.	6175.59	6204.53	627.98	0.1012	44
Mar.	6418.45	6414.88	574.81	0.0896	45
Apr.	4298.22	4308.04	331.48	0.0769	71
May	6221.85	6220.51	328.09	0.0527	123
June	6914.27	6915.34	211.50	0.0306	186
July	7666.10	7668.52	228.35	0.0298	185
Aug.	8372.73	8375.37	266.20	0.0318	195
Sept.	7896.75	7900.49	297.25	0.0376	156
Oct.	8291.34	8292.73	294.09	0.0355	161
Nov.	7128.69	7131.35	437.16	0.0487	118
Dec.	9352.04	9369.32	743.21	0.0793	92
Year	7453.76	7454.02	109.92	0.0147	1441

The problems encountered with the regression method dictate that comparison cannot be made on this basis alone. The regression variance estimator is unbiased only when the model in (3) is valid. The estimates for the cases where nonzero intercepts were found are biased estimates due to lack-of-fit components introduced by ignoring these intercepts. As illustrated in Fig. 1 and 2 this behavior is due to the variances associated with the catches at any one level of effort. Use of the residual plots for determining weights is sample size dependent and may require, as in the yellowtail case, pooling that ignores seasonal trends in catchability. Further there is no guarantee that the

TABLE 3. Jackknife technique of estimating the variance of catch per unit effort (SE: standard error, CV: coefficient of variation).

Month	Catch per day	Jackknife estimates	SE(R_J)	CV(R_J)	No. of trip components
Yellowtail flounder 1976					
Jan.	6473.71	6610.21	1978.03	0.2992	7
Feb.	5703.94	5756.38	864.54	0.1502	5
Mar.	6140.23	6217.57	820.84	0.1320	21
Apr.	6159.30	6161.75	307.01	0.0498	50
May	4737.41	4745.04	278.68	0.0587	70
June	5109.05	5817.94	1771.35	0.3045	7
July	2763.47	2785.89	573.72	0.2059	8
Aug.	4531.25	4880.24	1914.06	0.3922	5
Sept.	4277.31	4322.08	566.76	0.1311	10
Oct.	3948.69	3884.36	620.90	0.1598	16
Nov.	3213.38	3353.24	1041.37	0.3106	6
Dec.	6836.27	6962.43	248.33	0.0357	2
Year	5342.08	5344.45	189.41	0.0354	207
1977					
Jan.	—	—	—	—	—
Feb.	10269.48	10269.48	—	—	1
Mar.	6870.96	5714.37	3469.77	0.6072	2
Apr.	6535.06	6562.00	1230.36	0.1875	5
May	5934.68	5928.96	295.17	0.0498	44
June	5350.22	5346.52	335.52	0.0627	34
July	6563.53	6543.45	474.00	0.0724	41
Aug.	5838.38	5847.93	394.28	0.0674	45
Sept.	5400.01	5430.38	866.67	0.1596	15
Oct.	4916.27	4648.72	1621.17	0.3487	5
Nov.	8968.03	8942.65	673.68	0.0753	52
Dec.	8388.27	8384.92	965.07	0.1151	18
Year	6628.96	6626.64	200.21	0.0302	262
1978					
Jan.	9192.81	9131.66	1422.67	0.1558	6
Feb.	4488.92	4634.01	969.77	0.2093	3
Mar.	7596.98	7656.30	925.55	0.1209	6
Apr.	6431.97	6411.53	595.73	0.0929	38
May	7073.23	7035.55	580.61	0.0825	33
June	5163.22	5161.33	255.07	0.0494	32
July	6720.50	6700.00	748.82	0.1118	19
Aug.	7110.58	7089.23	466.72	0.0658	28
Sept.	8354.62	8330.11	780.23	0.0937	41
Oct.	11463.36	11436.06	688.14	0.0584	73
Nov.	8474.87	8460.16	429.26	0.0507	53
Dec.	7780.14	7831.03	1047.15	0.1337	14
Year	8267.59	8266.04	229.46	0.0278	346

variance structure and hence the type of regression estimator (as defined in (4)–(6)) will be the same from year to year. This will incur problems with respect to analysis of between time differences.

The Jacknife technique is model independent. For most of the sample sizes considered here the variance estimator is asymptotically unbiased.

I suggest, therefore, that the Jackknife estimator is preferred over the regression technique. The general utility of the method and comparative ease of application further support this suggestion.

Kulka (1979) has applied the Jackknife estimator discussed here to catch per unit effort data from the Foreign Observer program. Use of this technique demonstrated that the use of hours rather than days as units of effort provided more stable estimates, with respect to the variance of the estimate of catch per unit effort.

It should also be added that the data sets analyzed in this paper are ideal with respect to the detailed information available. Such complete information is usually not available. For any other data sets, if information on species catch and directed effort is available within a specific period of time, the Jackknife method will retain its utility.

Finally further work is required in order to determine if Tukey's postulate of a Student's-*t* distribution is valid for the data of the type considered here. If this can be established then equation (12) could be used as a pivotal value for confidence interval estimation and hypothesis testing.

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Origin of a Relict Population of *Salvelinus* in Bear Creek of the Alsek River Drainage, Yukon Territory

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SIKSTROM, C. B. 1980. Origin of a relict population of *Salvelinus* in Bear Creek of the Alsek River drainage, Yukon Territory. Can. J. Fish. Aquat. Sci. 37: 2352–2354.

A freshwater-resident population of *Salvelinus* was compared meristically and morphometrically with two forms of *Salvelinus* described by Cavender (1978). A comparison of the numbers of mandibular pores and branchiostegal rays, and gill raker morphology and head size revealed that the population of *Salvelinus* in Bear Creek corresponds to Cavender's specific distinction of a form which is generally characterized as anadromous *Salvelinus malma*. I suggest that the population of *Salvelinus* in Bear Creek was established from a natural colonization by formerly anadromous Dolly Varden char from the Gulf of Alaska.

Key words: Salvelinus, zoogeography, meristics, Yukon Territory, Kluane National Park

SIKSTROM, C. B. 1980. Origin of a relict population of *Salvelinus* in Bear Creek of the Alsek River drainage, Yukon Territory. Can. J. Fish. Aquat. Sci. 37: 2352–2354.

Les caractères numériques et morphométriques d'une population de *Salvelinus* résidant en eau douce ont été comparés à ceux de deux formes de *Salvelinus* décrites par Cavender (1978). Une comparaison du nombre des pores mandibulaires et des rayons branchiostèges, ainsi que la morphologie des branchicténies et la grosseur de la tête indiquent que la population de *Salvelinus* du ruisseau Bear correspond à la distinction spécifique établie par Cavender d'une forme généralement caractérisée comme anadrome *Salvelinus malma*. À mon avis, la population de *Salvelinus* du ruisseau Bear se serait établie à la suite d'une colonisation naturelle par des Dolly Varden jadis anadromes provenant du golfe d'Alaska.

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WHILE conducting ecological surveys for the proposed Alaska Highway Gas Pipeline, Beak Consultants Limited sampled a population of dwarf *Salvelinus* in Bear Creek, Yukon Territory (Fig. 1).[2] The following meristic and morphological characters were examined: the number of branchiostegal rays and mandibular pores, gill raker morphology, and the proportion of standard body length to head length.

Bear Creek originates in the Shakwak Valley and flows south into the Dezadeash River, within Kluane National Park, west of Haines Junction. The unusual geological history of the Alsek River drainage has been very important for the dispersal of fishes in the area (Lindsey 1975). The presence of a self-sustaining freshwater-resident population of *Salvelinus* in Bear Creek provided a special opportunity for further interpretation of the biological history of this region of Yukon Territory.

An account of the geological events in the area and a discussion of the likely dispersal routes of fish species in the Alsek drainage is given by Lindsey (1975). Most fish species in the Alsek drainage probably entered it from the Yukon River system during the time of Glacial Lake Champagne (circa 13500 B.P.). However, there was also access for anadromous species ascending the Alsek River from the Gulf of Alaska during a hypisthermal period lasting until about 250 B.P. Native tradition indicates that salmon formerly migrated into the headwaters of the Alsek and Dezadeash rivers. This assertion is supported by the presence of nonanadromous populations of kokanee (*Oncorhynchus nerka*) and rainbow trout (*Salmo gairdneri*) (neither of which occurs in the upper Yukon River) in headwater lakes of the Dezadeash River. Anadromous runs of both species ascend the Tatshenshini River (a tributary of the lower Alsek River) to its headwaters but neither ascends the main Alsek River which was blocked by an advance of the Lowell Glacier as recently as 125 B.P. This blockage likely prevented upstream spawning migrations of anadromous species. At present the blockage is gone, however, velocity barriers prevent the upstream movements of fish past the point of the previous blockage (Alaska Department of Fish and Game. Scientific investigations in Canada as per permit June 15, 1962 by Minister of Fisheries. On file with Department of Fisheries and the Environment, Vancouver, B.C.).

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[2] Specimens have been deposited in the National Museum of Natural Sciences, Canada.

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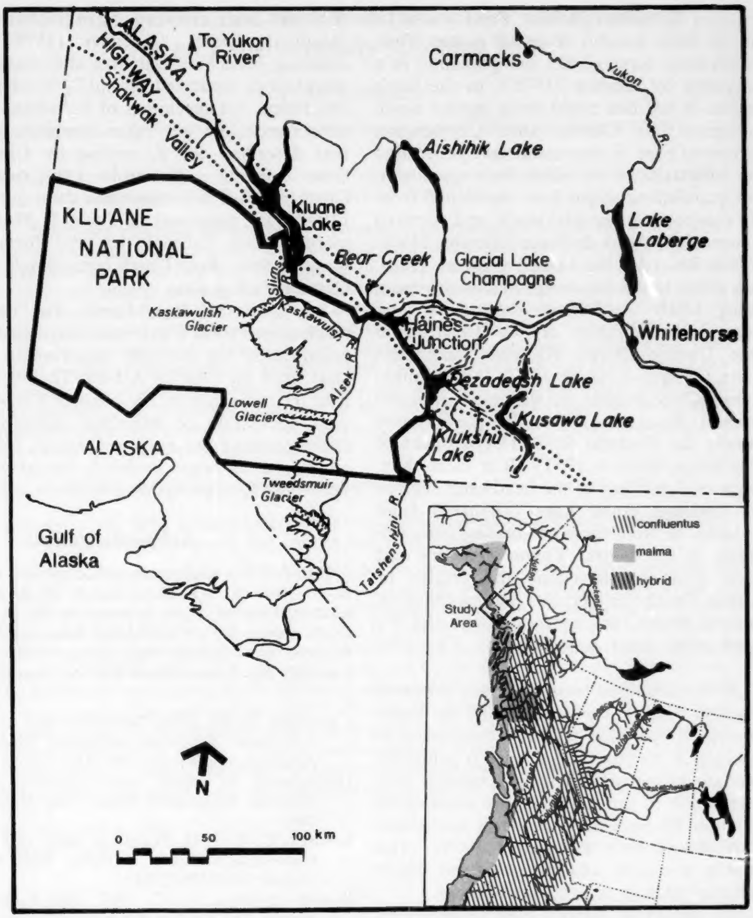
To Yukon River
ALASKA HIGHWAY
Shakwak Valley
Carmacks
Yukon R.
Aishihik Lake
KLUANE NATIONAL PARK
Kluane Lake
Lake Laberge
Slims
Bear Creek
Glacial Lake Champagne
Kaskawulsh Glacier
Kaskawulsh
Haines Junction
Whitehorse
Alsek R.
Dezadeash Lake
Lowell Glacier
Kusawa Lake
Klukshu Lake
ALASKA
Tweedsmuir Glacier
Gulf of Alaska
Tatshenshini R.
N
0
50
100 km
confluentus
malma
hybrid
Study Area
Mackenzie R.

FIG. 1. The Bear Creek study area in relation to the distribution of bull trout (*Salvelinus confluentus*) and Dolly Varden (*Salvelinus malma*) as described by Cavender (1978).

TABLE 1. Comparison of selected meristic and morphometric characters for *Salvelinus* from Bear Creek, Yukon Territory, the bull trout (*Salvelinus confluentus*)[a] and the Dolly Varden (*Salvelinus malma*)[a] from northwestern North America.

Taxonomic character	Bear Creek (*Salvelinus*)				Dolly Varden (*Salvelinus malma*)				Bull trout (*Salvelinus confluentus*)			
	n	Range	Mean	±SD	*n*	Range	Mean	±SD	*n*	Range	Mean	±SD
Branchiostegal rays	37	17–23	20.5	1.36	88	21.92–23.33	22.57	0.77	120	26.31–28.71	27.37	1.38
Mandibular pores	34	11–15	12.6	0.99	87	11.91–12.18	12.10	0.80	118	13.71–16.64	15.57	1.49
Proportion body length to head size	37	3.4–4.8	4.0	—	55	3.5–4.7	4.23	—	111	3.2–4.1 (4.7)[b]	3.73	—

[a] After Cavender (1978).

[b] One individual with abnormally small head.

The presence of *Salvelinus* in Bear Creek could be accounted for by three possible dispersal routes. First, these char could have survived the last glaciation in a refugium, suggested by Lindsey (1975), to the north and into Alaska. If so, fish could have moved south from the refugium into Glacial Lake Champagne. Second, anadromous runs of char could have penetrated the headwater tributaries of the Alsek drainage. Freshwater resident populations might have developed from this originally anadromous parental stock, and survived in the headwaters of the Alsek drainage following blockage of the Alsek River by the Lowell Glacier. Third, the Dezadeash River might have captured anadromous fishes including Dolly Varden, rainbow trout and kokanee, from the headwaters of the Tatshenshini River via the Unahini River, Klukshu Lake, and Dezadeash Lake (Wynne-Edwards 1947). An examination of National Topographic Series maps indicates that the Unahini River, to which Wynne-Edwards refers, is actually the Klukshu River (Department of Mines and Technical Surveys 1951). It is clear then, that populations of *Salvelinus* in the headwater regions of the Alsek drainage could have originated from anadromous stocks, or from races originating from unglaciated refugia in the central Yukon Territory and Alaska. In an effort to determine the origins of *Salvelinus* in Bear Creek the meristics and morphology of specimens from Bear Creek were examined and the data compared with those presented by Cavender (1978).

Cavender (1978) described two taxonomic forms of *Salvelinus*: the bull trout, *S. confluentus*, and the Dolly Varden, *S. malma*. These were formerly considered to be a single species, *S. malma*. The former is primarily an interior, nonanadromous form which probably survived glaciation south of the ice sheet and attained its present distribution by postglacial dispersal northward from the Columbia system (Cavender 1978). The latter is primarily a coastal anadromous form which likely survived glaciation in coastal water bodies.

The bull trout and Dolly Varden may be separated on the basis of shape and size of head, gill raker morphology, and numbers of branchiostegal rays and mandibular pores. Cavender (1978) reported that counting branchiostegal rays and examining gill raker morphology separated 90 and 98%, respectively, of the two forms. All specimens of *Salvelinus* examined from Bear Creek had gill raker morphology equivalent to that described for *S. malma* by Cavender (1978). Other meristic and morphometric data for the Bear Creek population compared to those given by Cavender (1978) are presented in Table 1. Morphological and meristic data indicate that the form of *Salvelinus* sampled from Bear Creek corresponds most closely to Cavender's *S. malma*.

I suggest that Bear Creek char represent a nonanadromous form which was established from a natural colonization by formerly anadromous Dolly Varden char from the Gulf of Alaska. The existing population is of interest scientifically because it was the only abundant population of *Salvelinus* sampled in the Alsek drainage along the proposed Alaska Highway Pipeline route, and its origin is closely linked with past glacial activity in Kluane National Park.

Acknowledgments

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Teratogenesis in Lake Trout (*Salvelinus namaycush*) in an Experimentally Acidified Lake[1,2]

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KENNEDY, L. A. 1980. Teratogenesis in lake trout (*Salvelinus namaycush*) in an experimentally acidified lake. Can. J. Fish. Aquat. Sci. 37: 2355–2358.

Embryonic mortality and morbidity were seen in an indigenous population of lake trout (*Salvelinus namaycush*) inhabiting a lake experimentally acidified over a period of 3 yr to a mean summer epilimnion pH of 5.84. The pH of the hypolimnetic zone where trout spend the summer and undergo gametogenesis was 6.2. Although fertilization appeared to be successful, 59% of eggs incubated in the acidified lake had died or failed to gastrulate by 15 d, and 60% of the surviving embryos displayed gross anatomical malformations. Prior to hatching only 6% of the eggs contained embryos and all were anomalous. In a control lake, 92.9% of eggs contained normal embryos prior to hatching. Both the volume and dry weight of eggs of fish inhabiting the acidified lake were significantly less than eggs from the control lake. When gametogenesis and fertilization occurred in the acid lake but embryogenesis occurred in untreated water in the laboratory, there was a 50% reduction in the viability of eggs of one fish by day 31, compared to controls.

Key words: lake acidification, teratogenesis, lake trout

KENNEDY, L. A. 1980. Teratogenesis in lake trout (*Salvelinus namaycush*) in an experimentally acidified lake. Can. J. Fish. Aquat. Sci. 37: 2355–2358.

Des embryons morts ou mourants ont été observés chez une population indigène de touladis (*Salvelinus namaycush*) d'un lac expérimentalement acidifié pendant une période de trois ans et amené à un pH estival moyen dans l'épilimnion de 5,84. Dans la zone hypolimnétique, où le touladi passe l'été et où se produit la gamétogénèse, le pH est de 6,2. Bien que la fécondation semble réussie, 59% des oeufs incubés dans le lac acidifié meurent ou ne subissent pas de gastrulation dans les 15 jours qui suivent, et 60% des embryons qui survivent exhibent des difformités bien visibles. Avant l'éclosion, seulement 6% des oeufs sont embryonnés et tous sont anormaux. Dans un lac témoin, 92,9% des oeufs contiennent des embryons normaux avant l'éclosion. Dans le lac acidifié, le volume et le poids sec des oeufs sont nettement inférieurs à ceux des oeufs du lac témoin. Quand la gamétogénèse et la fécondation se produisent dans le lac acide et que l'embryogénèse ait réussi dans de l'eau non traitée, en laboratoire, il y a réduction de 50% de la viabilité des oeufs d'un poisson au jour 31, comparativement aux témoins.

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THE loss of trout populations in lakes and rivers undergoing a gradual decrease in pH due to acid precipitation is well-documented (Jensen and Snekvik 1972; Beamish 1974; Beamish et al. 1975; Schofield 1975). Beamish (1975) has reported that lake trout (*Salvelinus namaycush*) populations become extinct at pH values below 5.0 and cease reproduction at pH 5.5. The loss of fish has been generally attributed to a failure of recruitment in acidified waters (Beamish 1975), however, it is as yet unknown where in the reproductive cycle of fishes depressed pH is exerting its deleterious effects and how. There is evidence that reproductively active fishes are more susceptible to reduced pH than nonbreeding adults (Anthony et al. 1977). Only a few laboratory studies have used semichronic or chronic exposure spanning an entire generation or reproductive cycle, but all have concluded that reproduction is impaired and that egg viability and hatchability are reduced at pH levels below 6.5 (Mount 1973; Menendez 1976; Craig and Baski 1977; Smith 1977). The present experiments were designed to evaluate the effects of reduced pH on reproduction and recruitment in an indigenous population of lake trout inhabiting a lake which has been experimentally acidified over a 3-yr period.

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[1] This investigation is part of a whole lake acidification experiment being conducted at the Experimental Lakes Area (ELA) in northwestern Ontario. Details of the experiment are given in papers published in Can. J. Fish. Aquat. Sci. 37(3), 1980.

[2] Presented at 6th annual Aquatic Toxicity Workshop, Freshwater Institute, Winnipeg, Man., 1979.

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Materials and methods — A whole lake acidification experiment is being conducted at the Experimental Lakes Area (ELA) in northwestern Ontario. Lake 223, a remote and previously untouched lake in the Precambrian Shield, has been gradually acidified from an original surface pH ranging from 6.5 to 7.0 in 1975, to pH 6.1 in 1977, and then to 5.75 in the spring of 1978. The mean surface pH over the summer was 5.84. Lake trout are cold stenotherms which are known to inhabit the hypolimnion during warm summer months. The lower hypolimnion of Lake 223 is anoxic, due to incomplete spring and fall turnover (Schindler et al. 1980). Lake trout are largely confined to the hypolimnetic zone below the thermocline and above the anoxic zone (K. Mills, Freshwater Institute, personal communication). The pH of this zone in August 1978 was 6.2 (9.6 mg $\mathrm{CaCO_3L^{-1}}$; 10.23 mg $\mathrm{O_2L^{-1}}$). Schindler et al. (1980) give complete seasonal and spatial chemistry data. The two control lakes are chemically similar to Lake 223 prior to acidification.

Ripe females and males were captured using finemesh gill nets, trap nets, and angling. Eggs from one female were mixed with milt from two to three males from the same lake, and fertilized in plastic tubs in water from their respective lakes. After 0.5 h the eggs were rinsed with freshwater and let stand overnight in covered tubs sitting in the lake. The day of fertilization was designated day 0 of the experiment. Eggs that had whitened by day 1 were considered to be infertile and were counted and removed. Percent fertilization success was calculated in this manner for at least five females from each lake. Since it was not assumed that all nonwhitened eggs were viable, they were designated "apparently viable." Two embryological experiments were then conducted. In the first experiment, eggs were incubated in situ. Apparently viable eggs from one Lake 223 female were placed in plexiglass containers which were then suspended 0.5 to 1 m above the spawning grounds in Lake 223. Similarly, eggs from one Roddy Lake female were incubated in Roddy Lake, a nearby, unpolluted lake. For each lake there were 12 incubators, each holding 50 eggs in individual chambers. On days 15, 25, and 30 after fertilization, incubators were sampled from each lake until at least 50 apparently viable eggs were obtained for embryological analysis. Because of the constraints of a remote field station, a winter sample was taken from both lakes on the same calendar day but on different days of incubation. Whitened eggs were counted and discarded. Apparently viable eggs were placed immediately in Davidson's fixative and subsequently examined under a dissecting microscope. Eggs were categorized as follows:

Dead-eggs which had whitened, eggs containing a periblast with a necrotic or degenerating blastodisc, or later in development, eggs containing no formed embryo (embryonic failures).

Blastodisc/morula — a solid, round disc of embryonic cells.

Early gastrula — distinct germ ring and terminal node.

Embryo — epiboly near completion, axial organization complete.

Eyed embryo — eye pigment is present.

Dysmorphic embryos — eggs containing live embryos that displayed gross external morphological malformations.

In the second experiment, the effects of lake acidification on gametogenesis and fertilization, as reflected in early embryogenesis, egg viability, and certain aspects of egg quality were investigated. Eggs obtained from fish inhabiting Lake 224 were used as controls in this experiment. Egg volume was measured on subsamples of 20 fertilized eggs from nine Lake 224 females and five Lake 223 females using the volume displacement method. Mean dry weight per egg was calculated after oven drying (100°C for 24 h) using a subsample of 20 apparently viable eggs from each fish. The variation in mean volume and mean dry weight of egg subsamples between fish from the two lakes was assessed using a one-way analysis of variance. The dried samples were analyzed for calcium, sodium, potassium, and phosphorus using methods described by Stainton et al. (1977). Approximately 300 apparently viable eggs from one of the Lake 223 females and one of the Lake 224 females were then placed in egg trays in 6-L tubs in the laboratory. The eggs from both lakes were incubated in untreated water from Roddy Lake and were maintained at 10°C. Whitened eggs were removed daily and recorded as egg mortalities. On days 4, 9, 15, 20, 26, and 31 of the experiment, 50 apparently viable eggs were removed, placed immediately in Davidson's fixative and examined subsequently under a dissecting microscope for differences in rate of development and in the incidence of gross, external malformations.

Results — The two control lakes, Lake 224 and Roddy Lake, are chemically similar to Lake 223 prior to acidification. All three lakes are oligotrophic and have very low buffering capacity.

Fertilization was highly successful in all samples of eggs obtained from Roddy Lake, Lake 224 and Lake 223 fish. Ninety-five to 98% of eggs from all lakes were apparently viable on day 1. Lake 223 egg volume was 77% that of Lake 224 eggs ($P < 0.01$). Similarly, the mean dry weight per Lake 223 eggs was only 76% of that of Lake 224 eggs ($P < 0.005$). There was no significant variation in Ca, Na, K, or P concentrations of eggs from the two lakes.

Table 1 summarizes the embryological failure observed in the in situ experiment. Compared to controls,

TABLE 1. Summary of embryological failure observed in lake trout eggs from Lake 223 (mean summer pH 5.84) compared to Roddy Lake (pH ≈ 6.6).

	Total embryonic mortality (% *n*)	Total surviving embryol	
		Dysmorphic embryos (% survivors)	Normas embryos (% *n*)
Roddy Lake (pH ≈ 6.6)			
Day 15 (*n* = 50)	2%	0%	98%
Day 25 (*n* = 100)	3%	3.1%	94%
Day 30 (*n* = 100)	7%	1.1%	92%
Winter sample:			
Day 65 (*n* = 99)	7.1%	0%	92.9%
Lake 223 (pH 5.84)			
Day 15 (*n* = 87)	59.8%	60%	16.1%
Day 25 (*n* = 198)	85.3%	37.9%	9.1%
Day 30 (*n* = 163)	83.4%	29.6%	11.7%
Winter sample:			
Day 59 (*n* = 151)	94%	100%	0%

by day 30 there was a 76% increase in the incidence of embryonic mortality and a 28% increase in the number of dysmorphic embryos in the Lake 223 sample. Typically, in the dysmorphic embryos, entire caudal segments were seen either detaching from the body of the embryo or imbedded on the adjacent periblast. Where the lesion was bilateral, a stump-like caudal region remained; where the amputations were unilateral, a hook-like caudal region remained. The extent and severity of these amputations varied from individual to individual. In addition to the high incidence of anatomical malformation, the surviving embryos from the acid Lake 223 were smaller and less well developed, particularly in the head region, compared to their counterparts from unpolluted Roddy Lake. In the day 65 sample from Roddy Lake, there were no anatomical defects detected among the surviving embryos. In contrast, 100% of the embryos in the day 59 Lake 223 sample were either dead or abnormal. When compared to Roddy embryos, the surviving Lake 223 embryos were small and edematous with a very short thick body and disproportionately large head.

When apparently viable eggs from Lake 223 and Lake 224 parents were incubated in untreated water in the laboratory, there was no difference between the rates of development of the two groups of eggs, as reflected in the onset and duration of major developmental events. However, only 24% of eggs from Lake 223 fish had gastrulated successfully by day 15 compared to 75% of eggs from Lake 224. This represents a very high loss among the progeny of Lake 223 fish due to early embryonic loss. By day 31, 74.5% of eggs from Lake 224 contained eyed embryos compared to only 28.6% of the eggs from Lake 223. Two Lake 224 eggs whitened and were removed, in contrast to 45 Lake 223 eggs.

Discussion — This study documents the embryological failure observed when gametogenesis, fertilization, and embryogenesis occur in a whole lake which has been experimentally acidified. Among the eggs of fish obtained from all three lakes, fertilization appeared to be highly successful. However, the eggs obtained from fish inhabiting the acid lake were significantly smaller and demonstrated a marked increase in the incidence of early embryonic mortality. Gametogenesis and fertilization in the acidified lake were associated with at least a 50% decrease in early embryonic survival even when embryogenesis occurred in untreated water. When the eggs from Lake 223 were returned to the lake for incubation there was an additional 26% early embryonic mortality attributable to lake acidification and a high incidence of malformation among survivors. Prior to hatching there were no normal embryos in the incubators in Lake 223 whereas in the control lake 93% of embryos were morphologically normal. Impaired egg viability following gametogenesis and embryogenesis in acidified water has been reported in other species (Mount 1973; Menendez 1976; Craig and Baski 1977; Smith 1977). These observations demonstrate that the effects of lake acidification on gametogenesis and fertilization alone make significant contribution to early embryological failure. The mechanism underlying this phenomenon is not known. Fertilization and water hardening may be a critical period for egg sensitivity to reduced pH, at which time the influx of acidified water may contribute to the observed early embryonic mortality. It has been documented elsewhere, however, that gametogenesis is severely impaired by small reductions in pH associated with increased $p\mathrm{CO}_2$ (Ruby et al. 1977, 1978).

These observations indicate that acidification of a lake can have profoundly damaging effects on lake trout reproduction. Despite this there was some recruitment of viable young-of-the-year into the Lake 223 trout population from the 1978 spawn (K. Mills, Freshwater Institute, personal communication). It is evident, therefore, that my results do not indicate all of what is going on in the lake itself. It is possible that in working with eggs from a relatively small proportion of the fish in Lake 223 (total of five in this and other studies in 1978), I have missed the contribution that a few more resistant individuals can make to recruitment. It is also possible that the methods of incubation used represent an additional stress to an already stressed organism such that the results are somewhat exaggerated. Nonetheless my results imply that even in the absence of detectable damage to the existing population, the reproductive capacity of lake trout can be severely impaired by reductions in hypolimnion pH as small as 0.5 units from normal values in combination with the associated geochemical changes. That there is a critical pH for lake trout reproduction and survival is supported by the results of a survey of 109 lakes in the ELA area, which revealed that only two lakes with a summer surface epilimnion pH of 6.3 or below supported lake trout populations (Beamish et al. 1976). Further support is obtained by inventory data collected by the Province of Ontario (Martin and Olver 1976) which show that only 9% of the lakes in Ontario which contain lake trout have pH values less than 6.0.

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Acoustically Derived Estimate of the Size Distribution for a Sample of Sperm Whales (*Physeter catodon*) in the Western North Atlantic

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Adler-Fenchel, H. S. 1980. Acoustically derived estimate of the size distribution for a sample of sperm whales (*Physeter catodon*) in the western North Atlantic. Can. J. Fish. Aquat. Sci. 37: 2358–2361.

Acoustic determination of sperm whale length based on measurement of the interpulse interval (IPI) of the characteristic multipulse sound click was used on a sample of 4000 clicks in 193 click series recorded in the North Atlantic. The analysis of IPI could be done with reasonable reproducibility using a minimum of equipment: a tape recorder, filter, and oscilloscope. Criteria were developed to choose suitable clicks for analysis. In the click sample, 11% met the criteria for analysis, and were contained in 41 click series, of which 22 had a unique IPI. The IPIs in the 41 series ranged between 1.6 and 8.0 ms, and corresponded to a predicted size range of 7–22 m. This is consistent for the size range reported for the western North Atlantic.

Key words: bioacoustics, sperm whale, *Physeter catodon*, size determination, click, interpulse interval

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Une méthode acoustique de détermination de la longueur des cachalots, fondée sur la mesure de l'intervalle entre les pulses d'un clic (IPI, « interpulse interval ») à même le clic de multipulsation caractéristique a été utilisée sur un échantillon de 4 000 clics dans 193 séries de clics enregistrés en Atlantique nord. L'analyse de l'IPI a pu être effectuée avec un degré raisonnable de reproductibilité, avec un minimum d'appareils : un magnétophone, un filtre et un oscilloscope. Des critères de choix adéquats de clics aux fins d'analyse ont été établis. Dans l'échantillon de clics, 11% rencontrent les critères d'analyse et se trouvent dans 41 séries de clics, dont 22 ont un IPI unique. Les IPI dans les 41 séries varient de 1,6 à 8,0 ms et correspondent à une gamme de tailles prédites de 7 à 22 m. Ceci est conforme aux tailles signalées dans l'ouest de l'Atlantique nord.

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To evaluate the age structure of a population, it is necessary to find reliable characteristics that provide information on absolute or relative age (Cushing 1968). For the sperm whale, *Physeter catodon*, total body length was used by Matthews (1938), Nishiwaki et al. (1963), and Berzin (1972). Norris and Harvey (1972) proposed a remote acoustic method for estimating individual whale length, which was expressed by Møhl et al. (1976) with the following second-order polynomial equation:

$$(1)\quad TL = 0.86 + 4.53\ IPI - 0.142(IPI \times 1.3)^2$$

where TL is total body length in metres, and IPI is the *interpulse interval*, the time in milliseconds between homologous events in the sperm whale click, and which is assumed to be constant for each individual whale (Fig. 1).

The acoustic size determination method is still tentative. Since it is difficult to obtain direct verification of this method through direct encounters with the whale while recording its clicks, it is desirable to gather as much indirect evidence as possible for the method's feasibility and validity. Thus, I have used the acoustic approach on a sample of recorded clicks from the western North Atlantic to evaluate the minimum instrumentational requirements for click analysis, criteria for the selection of clicks for analysis, and the correlation between acoustically determined size estimates and size ranges previously obtained from catch statistics.

Materials and methods — Approximately 4 h of sperm whale click recordings made in the western North Atlantic from the R/V *Trident* (cruises TRI-4-1, 17/07/63, TRI-17-7, 08/08/68, TRI-17-10, 09/08/68, TRI-22-5, 17/01/71) were obtained through the courtesy of Drs H. Winn and P. Perkins, University of Rhode Island. These tapes were analyzed using a Uher 4200 Report tape recorder, a Krohn-Hite 3550 filter centered at 6 kHz (BP: 10 kHz), and a Gould Advance OS 4000 digital-storage oscilloscope.

Approximately 4000 clicks were examined in the context of 193 click series. A single click series is defined as any number of clicks produced in a continuous and more or less unique rhythm, terminating when the time interval between one click and the next is at least 10 times the preceding interval.

The interpulse intervals (IPI) in the individual clicks were measured on the oscilloscope by choosing one to several marker peaks in the pulses (Fig. 1). The clicks were chosen for analysis by the following confidence ranking scheme (cf. Fig. 1 for click nomenclature):

	Points
Click in context of series	1
Click not in context of series	0
P_2 with $\geq$ 2:1 S/N	1
P_2 with < 2:1 S/N	0
P_3 with $\geq$ 2:1 S/N	2
P_3 with < 2:1 S/N	1
P_1 with $\leq$ 2 regular cycles	2
P_1 with > 2 regular cycles	1
Without "S" components	2
With "S" components	1

+1 point if >3 pulses with $\geq$2:1 S/N.

Anytime a "0" was reached in the scheme, the click was rejected. Otherwise, all clicks were used. The signal to noise ratio (S/N) was measured by comparing the maximum peak height in the pulse to the maximum peak height in the IPI. Possible "S" components were evaluated by their amplitudes and phase relationships relative to the preceding pulse. Only series containing at least three "analyzable" clicks were used in the final calculations with IPI.

Whale size was calculated from equation 1 using the mean IPI_1 from individual series. This distribution was compared to that reported by Mitchell (1974) for the Nova Scotia and Newfoundland whale fisheries.

In order to estimate the variability of the IPI measurements, all series on the same cut of tape, and with the same mean IPI_1 were pooled and considered to be produced by the self-same whale. In addition, all IPI measurements were used (IPI_1, IPI_2 . . . [and] IPI_n), and standard deviation calculated.

Results — Of the total number of clicks, about 11%, or 424 met the criteria for analysis, and were contained in 41 series (21% of total available) of which 22 had unique intervals. Of the 41 series, 34% contained only 3 clicks meeting the analysis criteria, 47%

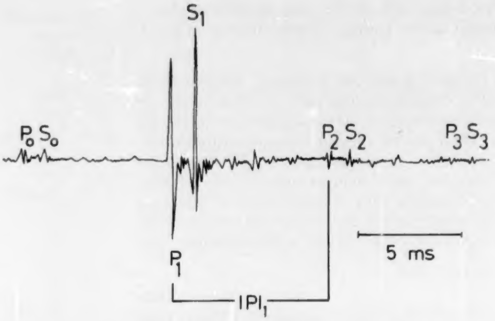

FIG. 1. A diagrammatic sperm whale click. The components are indicated as follows: P_0, a low amplitude event in some clicks, and not used in analysis; P_1–P_3, the regular pulses in the click; IPI, the interval between two consecutive pulses, measured marker peak to marker peak; S_1–S_3, assumed "reflections" of the P-pulses.

contained between 4 and 15 clicks, and 19% contained over 15 clicks.

The acoustically determined size distribution is compared to the size distribution reported by Mitchell (1974) in Fig. 2. The range reported by Mitchell is significantly narrower than the acoustically determined one. The mean length in Mitchell's sample is 14.4 m; for the *Trident* sample, it is 15.6 m for the entire sample, and 17.1 m for the sample from the more northern waters.

The IPI measurements for any single whale for any number of series varied up to 10% of the mean IPI (Table 1). Within a single multipulse click, IPI measurements never varied more than 0.25 ms.

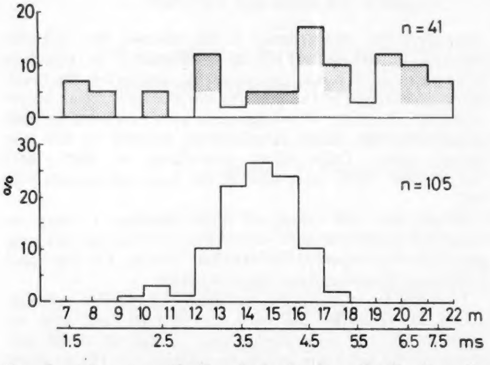

FIG. 2. The acoustically derived size distribution for sperm whales (upper) and the size distribution reported by Mitchell (1974) for the Nova Scotia fishery. The strippled area in the upper histogram shows the individuals from the southern waters (Bermuda and the Caribbean), while the unshaded area represents the more northern waters (Labrador and Newfoundland) and can be compared to Mitchell's sample below. The double abscissa is in milliseconds, relevant for the upper histogram, and metres, relevant for both distributions.

TABLE 1. IPI measurements from series of sperm whale clicks reported as mean IPI ± standard deviation (SD).

Mean IPI (ms)	SD	Range (ms)	TL (m)	*n* (IPI)
8.0	0.13	7.5–8.0	21.7	45
7.8	0.29	7.5–8.0	21.6	11
7.5	0.00	—	21.3	5
7.2	0.25	7.0–7.5	21.1	9
6.7	0.34	6.0–7.5	20.5	146
6.5	0.50	5.8–7.0	20.2	7
6.0	0.25	5.5–6.5	19.4	32
5.8	0.15	5.7–6.5	19.1	15
5.0	0.07	4.8–5.0	17.5	13
4.8	0.27	4.3–5.0	17.1	144
4.7	0.06	4.7–5.0	16.9	39
4.7	0.23	4.3–5.0	16.9	36
4.4	0.05	4.0–4.5	16.2	13
4.2	0.12	3.8–4.5	15.6	235
3.9	0.14	3.8–4.0	14.9	5
3.3	0.27	2.5–3.8	13.1	68
2.5	0.00	—	10.7	6
2.4	0.16	2.3–2.5	10.3	7
1.9	0.19	1.8–2.0	8.7	5
1.9	0.16	1.8–2.3	8.7	11
1.6	0.11	1.5–1.8	7.3	5
1.6	0.15	1.5–2.0	7.3	11

Discussion — The confidence ranking criteria for click selection suggest the minimum requirements to be met by a single click for analysis; that is, it should be in a series with the first two pulses having a greater than 2:1 S/N. The use of several confidence categories could easily be devised, and would be relevant in the context of a larger sample. Each additional pulse in a click with an acceptable S/N increases the confidence of the IPI measurements, assuming that the IPI varies only because of factors outside the whale, such as attenuation of the click, signal reflections, or other sound propagation losses. The 0.25 ms variation in a single click, however, probably arises from marker peak ambiguities and reading errors on the oscilloscope. Peak ambiguity becomes more of a problem as the number of cycles in a pulse increases. With few cycles, both peak position in the pulse and relative amplitude can be used. With more cycles, it is difficult to notice if a specific peak has fallen into the noise.

That the click be contained in a series, and that at least three clicks be readable in any series is important. A blow on the ship's hull, the training of a hydrophone, or biological sounds could produce multipulse recordings, but such events rarely occur in regular series.

"S" components (possibly surface reflections) generally obscure the information in the regular "P" pulses, and may be mistaken for a "P" pulse. If a suspect pulse has an amplitude approximately the same as the preceding pulse, and this event occurs at regular intervals through the click, it is diagnosed as an "S" component. It is generally less easy to see if the pulse has the characteristic phase shifted waveform. In the case where "S" and "P" pulses overlap, there are obvious peculiarities in waveform and amplitude. However, with a high S/N, the effects of the "S" components are minimized.

That only 21% of the series met the criteria for analysis could possibly reflect the recording method. The R/V *Trident* has its hydrophones placed more or less directly on her hull (Perkins 1966), which could possibly increase the number of reflections in the click. It would be advantageous for this type of analysis that the hydrophones be as far from all reflecting bodies as possible. In addition, the 21% figure was derived from the total number of series on the tape. Many whales click simultaneously, off-axis to the hydrophone, and these background series with a low S/N are included in the total.

The acoustically derived size range from the *Trident* sample presents no sizes that can be considered unrealistic (Berzin 1972). The sample, as indicated in Fig. 2, is comprised of individuals from both southern and northern waters. In the southern waters (stippled area), the entire size range would be expected, since this is where sperm whales mate and breed (Berzin 1972). The portion of the sample directly comparable to Mitchell's shows some discrepancies; the mean length is higher, and there are a disproportionate number of larger whales. This skewed distribution could be attributed to the small sample size ($n = 18$). The number of whales over 17 m could be from an intrinsic error in the equation for size calculation, a sampling artifact, or a real phenomenon. Equation 1 is based on the relation between head length and total body length given by Nishiwaki et al. (1963), and is known only for the 9–17 m TL range. The number of whales over 17 m has declined in recent years due to the overfishing in the past, but it is claimed that some of the older, larger solitary bulls can still be found (Berzin 1972). Møhl and Amundin (Aarhus University, Aarhus, Denmark, personal communication) have recently recorded clicks from a 21 m whale, so although whales this size are rare, they could be expected. An especially vocal whale may also bias the sample. Because each series is considered as produced by a single whale, one producing many series would appear to be many whales. Watkins and Schevill (1977) report that there may be only one vocalizing whale in an otherwise silent group just beneath the surface, or conversely, that a whole group may click simultaneously. Possibly, with further validation of the acoustic method, which would require direct measurement of the individuals recorded, there will be another size structure than indicated by catch statistics.

The acoustic method of size determination takes both a minimum of equipment and training. Thus, it could be used to monitor whale populations and will give an estimate of population structure without removing members of the population. The obvious limitation of the method is, of course, that it only samples those whales that choose to click. These results, however, offer evidence that the acoustic method has a good deal of potential.

Acknowledgments — I gratefully acknowledge Drs H. Winn and P. Perkins for supplying the recordings, Bertel Mohl for valuable help and suggestions, and Tom Fenchel for helpful critique and figures.

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Possible Sexing Technique for Humpback Whales (*Megaptera novaeangliae*)

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JURASZ, V. P., D. MCSWEENEY, AND C. M. JURASZ. 1980. Possible sexing technique for humpback whales (*Megaptera novaeangliae*). Can. J. Fish. Aquat. Sci. 37: 2362–2364.

By comparing photographs of humpback whales (*Megaptera novaeangliae*) photographed at the peak of their arch during a dive, we found some to be smooth and others to be scalloped middorsally caudal to the dorsal fin. Out of 410 photographs taken in southeast Alaska and Hawaii, 66% were found to be smooth and 34% scalloped. All females with calves were smooth. One pregnant female was smooth and only one female who was pregnant was slightly scalloped. One known male was scalloped and one "singer" on the Hawaiian breeding grounds was scalloped. We suggest that the smoothness or scalloping of this region is a morphological feature and can be used with reasonable accuracy to determine sex in humpback whales.

Key words: humpback whales, morphology, sex

JURASZ, V. P., D. MCSWEENEY, AND C. M. JURASZ. 1980. Possible sexing technique for humpback whales (*Megaptera novaeangliae*). Can. J. Fish. Aquat. Sci. 37: 2362–2364.

En comparant des photographies de jubartes (*Megaptera novaeangliae*) prises au moment où l'arc dorsal est à son maximum dans une plongée, on a constaté que certains arcs étaient lisses, alors que d'autres étaient échancrés mi-dorsalement à l'arrière de la nageoire dorsale. Sur 410 photographies prises dans le sud-est de l'Alaska et à Hawaii, 66% sont lisses et 34% échancrées. Chez toutes les femelles accompagnées de leur veau, l'arc est lisse. Une femelle enceinte était lisse et seulement une femelle enceinte était légèrement échancrée. Une baleine de sexe mâle connu était échancrée, de même qu'un « singer », sur les lieux de reproduction d'Hawaii. Le caractère lisse ou échancré de cette région est une particularité morphologique qui pourrait être utilisée avec une précision raisonnable pour déterminer le sexe des jubartes.

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IN both the northern and southern hemispheres, Tomilin (1967) found that some sexual dimorphisms exist in humpback whales (*Megaptera novaeangliae*), for example, females differed from the males in having a more elongated rostrum and in having a greater number of throat pleats than males. Scammon (1874) suggested that females have fewer tubercles on the lower lip than do males. More recently, Winn and Winn (1978) have suggested that the "singer" humpback whale in calving areas may be a male, and have devised a method for determining sex of humpback whales through an examination of a live skin sample (Winn et al. 1973).

During 13 yr of close observation of humpback whales, we have noticed that the profile of the region extending from the dorsal fin to the caudal peduncle appears to be sex related. We analyzed photographs of the dorsal hump of humpback whales taken from two regions of southeast Alaska (Glacier Bay and Frederick Sound from 1967 to 1979 and from one region in the Hawaiian Islands from 1977 to 1979). The ridge of the dorsal hump which extends from the dorsal fin to the caudal peduncle was examined for smoothness or scalloping when the whale was photographed at the peak of its arch during a dive. Figures 1 and 2 present examples of two archings, smooth and scalloped.

Assuming that the adult consistently accompanying a calf is a female, photographs of 21 adults presumably female whales with calves (12 from Alaska and 9 from Hawaii) were found to be smooth in this region before diving. We were unable to evaluate all of the calves because the calves did not always come far enough out

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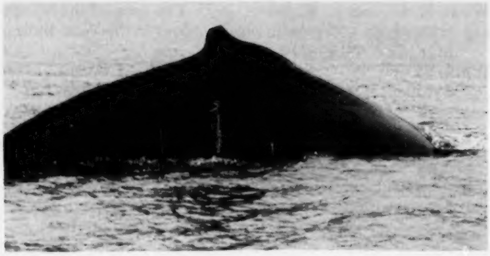

FIG. 1. A humpback whale with a smooth back, a characteristic of most females.

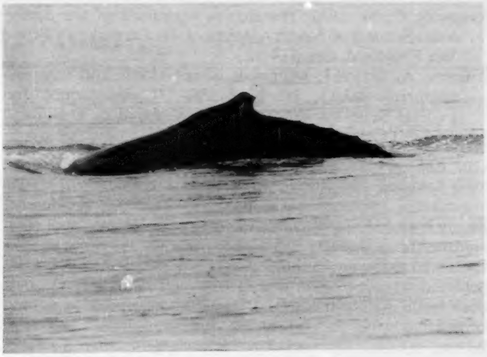

FIG. 2. A humpback whale with a scalloped back, a characteristic of most males.

of the water, but 6 were smooth and 3 were scalloped. One of the scalloped calves was photographed in Hawaii and the other two in Alaska. Of the whales examined in Hawaii, the only one that was determined by passive acoustical recording techniques to be a "singer" was scalloped.

A confirmed male (the penal and anal openings were clearly seen on the ventral surface) in the motion picture "Gentle Giants of the Pacific," filmed by Alfred Giddings for Survival Angliae Ltd. of London, was scalloped. Also in the film, all of the presumably female whales with small calves were smooth as were those determined to be females by viewing their ventral sides.

In Sitka, Alaska, a dead, nonpregnant female was found to be smooth when artificially arched with a large crane. The whale had been struck by a large vessel 12 h before it was examined. Some bloating was evident and could be considered as partially causing the smooth appearance.

Overall we examined 410 photographs of humpback whales at the moment of high arch. Of these 66% were smooth and 34% were scalloped. Our figures indicate that using random sampling throughout a feeding season in southeast Alaska, one can be 95% confident of finding 66 ± 1% of humpback whales with smooth backs and 34 ± 1% with scalloped backs. The sex ratios determined by catch statistics and fetal records were found to be nearly equal in both the northern and southern hemispheres, but there was a slightly higher proportion of females in the North Pacific (Tomilin 1967).

Out of 36 photographs taken from September to November (late in the season since feeding begins in May and June in southeast Alaska), 70% of the sample were smooth and 30% were scalloped. Thus even 4 mo into the feeding season, one can be 95% confident of finding 70 ± 3% with smooth backs and 30 ± 4% with scalloped backs. The sample size of 36 whales is small but does serve to examine any change in morphological features as the whales feed.

Two whales, sighted in Glacier Bay, summer 1977 were apparently pregnant, later being photographed accompanying calves off Hawaii during winter 1977–78 (Darling and Jurasz 1979). Of these two whales, one was smooth and one was slightly scalloped. This was the only suspected female that was scalloped.

Examinations of blubber thickness during whaling years indicated that blubber layer was thicker in females, pregnant females and calves than in males. We believe that this thicker layer of blubber may show itself in the area extending from the dorsal fin to the caudal peduncle, causing this area to be smooth in adults if they are females and scalloped if males.

The scalloping does not appear to be affected by age because calves were found to be scalloped and smooth both on Hawaiian breeding grounds and on Alaskan feeding grounds. Nor does the scalloping appear to be affected by length of time feeding because even toward the end of the feeding sason, 30 ± 4% were still found to be scalloped. Conversely, this region of blubber does not appear to be affected by the stress of nursing or fasting.

We suggest that the scalloping is a morphological feature and can be used to determine sex in humpback whales.

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LETTERS/LETTRES

Comment on Deriso's Delay-Difference Population Model

Usually letters to this *Journal* carry criticism of recent papers. I wish to compliment R. B. Deriso for what may be the most important contribution to fisheries population theory in the last two decades.

Deriso (1980) has shown that Beverton-Holt type age structure models can be collapsed into a simple difference equation format reminiscent of surplus production models like Schaefer's. Growth, survival, and recruitment parameters are preserved in the formulation, rather than being replaced with aggregated logistic growth parameters. So the difference equation provides the realism of age structure analyses, yet the simplicity for parameter estimation and optimization of surplus production analyses. In short, it has the good features of both approaches, and should quickly replace them for most practical applications.

Perhaps most important, Deriso's equations provide a unified framework for using catch and effort data in conjunction with more detailed assessments on growth, survival, and recruitment. We can now see much more clearly whether detailed studies are worthwhile, relative to assessments based solely on catch and effort data; we can begin to do sensible decision analyses on how to invest in alternative assessment studies. Deriso suggests that his estimation scheme based on catch/effort data can be cast in a Bayesian framework, with some parameters assigned prior probability distributions based on independent assessments. This is indeed feasible and can be accomplished by a simple modification of standard nonlinear estimation algorithms. This will be especially useful in the incorporation of growth data; Deriso notes that growth and natural mortality effects cannot be adequately separated using only catch/effort data.

Deriso's equations will provide a rich area for further research, particularly for statisticians with courage enough to tackle nonlinear estimation problems, and for those of us concerned with adaptive management strategies. I recommend the paper most highly for anyone seeking research problems in fishery dynamics. — *Carl J. Walters, Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C. V6T 1W5.*

DERISO, R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37: 268–282.

BOOK REVIEWS/COMPTES RENDUS

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Handbook of Phycological Methods. Physiological and Biochemical Methods. *Edited by Johan A. Hellebust and James S. Craigie (Sponsored by the Phycological Society of America, Inc.). Cambridge University Press, New York, NY. 1978. xiv + 512 p. $29.95 U.S.*

This handbook, edited by two of Canada's leading plant physiologists/biochemists, will prove an especially valuable resource for the experimental phycologist who often has only a limited background in biochemistry or experimental cell biology. It is a compendium of some of the simplest and most generally accepted methods employed today, neatly organized in 46 chapters by about as many contributors from universities and research institutions in the USA, Canada, Europe, and Japan. (Since the volume was sponsored by the Phycological Society of America, Inc., almost all of the suppliers for chemicals and equipment, listed on p. 491–494, are in the USA or Canada.) There are sections on the isolation of organelles and membranes (53 p.), analyses of chemical constituents (150 p.), enzymes (60 p.), physiological and biochemical processes (132 p.), nutrients (48 p.), ion content and transport (28 p.), and inhibitors (12 p.). There are excellent indexes of subjects, authors, and taxa, and for each chapter there are references with full titles (which we consider to be space well spent). The procedures outlined are adequately described, with details specified for a particular system (e.g. PEP carboxylase for a blue-green alga, RUDP carboxylase for a species of *Chlamydomonas*), but most are of general applicability with only minor modifications needed. The authors list the equipment required, describe methods for preparing the reagents, and suggest experimental protocols, etc. Many sections include a discussion of the limitations and advantages of the preparative or analytical principles involved. Choices had to be made, of course. The recommended method for protein determination is not that of Lowry, nor is the anthrone method recommended for carbohydrates, but reasons are given for the selection made. Thus, this is not simply a "cookbook" manual; each chapter provides a good starting point for techniques which an experimenter can proceed to modify when necessary, and indeed, in many chapters, there are suggestions for such modifications.

Most of the experimental approaches are quantitative as well as qualitative. Would it have been out of place to include a chapter on the ways by which one might best express one's results? Per cell or unit length of filament? Per unit wet weight, dry weight, or ash-free dry weight? Per unit cell protein or chlorophyll *a*? Answers to such questions must depend of course on the ultimate objectives of the researcher; choices should not be made merely on the basis of ease or expediency.

If we have to criticize something about this admirable work, we might perhaps point out its microbiological bias. More than 80% of this book deals with methods for dealing with unicellular or small filamentous forms. This is understandable, of course. The so-called "micro-algae" frequently possess attractive features for experimental research, such as ease of manipulation and short generation times. (The word "micro-algae" is a bastard formation that we shall probably have to live with.) But those of us who also work with larger seaweeds sometimes face additional problems of quantification, homogenization, dispersal by sonication, etc., for which this book gives insufficient guidance. Furthermore, many seaweeds are slimy or astringent, or both, and the magnitude of the obstacles caused by mucilages and tannins can only be appreciated by one who has tried to get organelles or enzymes out of, say, *Fucus*. Chapters in Colowick and Kaplan's "Methods in Enzymology," Volumes 1* and 31** in particular, should help the phycologist to resolve many such problems. Perhaps additional sections on these subjects might be added when Hellebust and Craigie prepare their second edition. Moreover, problems of uptake of nutrients, or the effects of inhibitors, are rendered much more acute when we have to consider masses of algal tissue which may be several millimetres thick. It is regrettable, but understandable, that all of the algae tabulated in the chapter on "Inhibitors used in studies of algal metabolism" are unicells or filaments only one cell in width.

The binding is firm, the paper good, the print clear, and there are almost no misprints. This is an excellent publication; no experimental phycologist can afford to be without it.

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*COLOWICK, S. P., AND N. O. KAPLAN, [ED.]. 1955. Methods in enzymology. Vol. 1. General preparative procedures (Section 1): 1–60 approx. (Many authors).

**COLOWICK, S. P., AND N. O. KAPLAN, [ED.]. 1974. Methods in enzymology. Vol. 31. Overcoming problems of phenolics and quinones in the isolation of plant enzymes and organelles. W. D. Loomis. (Section 4A:54): 528–543.

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April–July/avril–juillet 1980

***British Marine Amphipoda: Gammaridea.** *R. J. Lincoln. British Museum (Natural History), London, UK. 1980. 658 p. £50.00.* (This massive monograph is the first comprehensive and illustrated text to be published in more than a century on British gammaridean amphipods, a group considered to be notoriously difficult to identify.)

***Trout Farming Manual.** *John P. Stevenson. Fishing News Books, Farnham, Surrey, England. 1980. xi + 186 p. £9.75.* (This well-illustrated manual on trout farming is designed basically for the beginner, although there is much of use to the experienced aquaculturist. Like all of the books from this publisher, it is well designed for the target user.)

***Theory and Practice of Eel Culture.** *Isao Matsui. (Translated from Japanese.) Published for the U.S. National Marine Fisheries Service, and the U.S. National Science Foundation by Amerind Publishing Co. Pvt. Ltd., New Delhi, India. 1979. vii + 133 p. No price available.* (This short book is a practical description of the culture of *Anguilla japonica* and *A. marmorata* in Japan.)

***American Journal of Physiology: Regulatory, Integrative and Comparative Physiology. Volume 7, No. 2.** *Edited by F. E. Yates. The Jean Maetz Memorial Issue on the Chloride Cell. 1980. p. R139-R276. No price.* (The issue contains 19 papers in honor of the late Jean Maetz, who was killed in an automobile accident in August 1977.)

***The Biology and Physiology of the Living Coelacanth.** *Edited by John E. McCosker and Michael D. Lagios. Occasional Papers of the California Academy of Sciences, No. 134. 1979. 175 p. $10.00.* (This book is a collection of papers on *Latimeria*.)

Inland Fishes of Washington. *Richard S. Wydoski and Richard R. Whitney. University of Washington Press, Seattle. 1980. xxxii + 220 p. + 76 color plates. $8.95 (paper), $17.50 (cloth).* (This book consists of keys and life histories of the 76 species of freshwater fishes of Washington; it is aimed at a wide audience, including fishermen, students, biologists, and environmentalists.)

***Handbook of Phycological Methods. Developmental & Cytological Methods.** *Edited by Elisabeth Gantt, Cambridge University Press, New York. 1980. xii + 425 p. $29.95.* (This is the third in the series of phycological methods handbooks — see this issue for a review of the second volume on Physiological and Biochemical Methods.)

***Prairie Surface Waters. Problems and Solutions.** *Edited by Don T. Waite. Proceedings of the 1979 Prairie Aquatic Research Conference, Regina, 1979. Great Plains Research Center, Water Studies Institute, Saskatoon. 1980. ii + 102 p. $7.00.*

Diseases of Marine Animals. Volume 1. General Aspects. Protozoa to Gastropoda. *Edited by O. Kinne. John Wiley & Sons, New York. 1980. xiii + 466 p. $70.00.* (This is the first volume in a four-volume treatise, addressed to researchers, teachers and students of pathology, parasitology, ecology, fisheries biology, and aquaculture of marine animals.)

***Charrs. Salmonid Fishes of the Genus *Salvelinus*.** *Edited by Eugene K. Balon. Dr W. Junk bv Publishers. The Hague, The Netherlands. 1980. ix + 928 p. $250.00 Can.* (This massive treatise is Volume 1 in the publishers new series, Perspectives in Vertebrate Science.)

Bread Upon the Waters. The developing Law of the Sea. *Charles Fincham and William van Rensburg. Turtledove Publishing, Jerusalem, Israel. 1980. xvi + 249 p. $17.50.*

Management and Analysis of Biological Populations. *Bean-San Goh. Developments In Agricultural and Managed-Forest Ecology, 8. Elsevier Scientific Publishing Co., Amsterdam. 1980. ix + 288 p. $75.50 U.S.* (A highly-advanced mathematical text devoted to the application of Liapunov and Liapunov-like functions to nonlinear population models with respect to realistic perturbations and stability. An extensive mathematical background is required of the reader.)

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[1] Entries in this list *not* marked by an asterisk are available for review by interested readers for a 3-month period from the time of publication of the list. For information, please write to the Book Review Editor.

[1] Les ouvrages inclus dans cette liste et *non* accompagnés d'un astérisque peuvent être mis à la disposition de lecteurs intéressés qui voudraient en faire l'analyse, et ce, pour une période de 3 mois à compter de la date de parution de la liste. Pour plus de renseignements, veuillez écrire au rédacteur des Comptes rendus.

ANNOUNCEMENTS/AVIS

Ocean Pollution 1981

The Woods Hole Oceanographic Institution, Massachusetts together with the Bedford Institute of Oceanography, Dartmouth, Nova Scotia are cosponsoring this international conference on chemical contamination of the Northwest Atlantic Ocean. It will be held October 19–23, 1981 at the Bedford Institute of Oceanography. The conference co-organizers are Dr J. Farrington (Woods Hole Oceanographic Institution) and Dr J. H. Vandermeulen (Bedford Institute of Oceanography).

Through invited and contributed papers, the conference will focus on the state and processes of chemical contamination of the marine environment of the northwest Atlantic offshore. The presence and detection of foreign chemicals (fossil fuels, hydrocarbons, synthetic organics, pesticides, heavy metals) in sediments, waters, and organisms in the world's oceans is a potential problem that needs to be assessed. The sessions will concentrate on inputs and processes controlling the movement of contaminants and on the problem of their recognition and detection. A special keynote session of invited speakers on radionuclides in the marine environment will also be included. Discussion will focus on contaminant reservoirs and residence times, levels and turnover/accommodation, and on sediment–water interaction processes affecting these. There will be special emphasis on speciation and mobility of contaminants especially as relating to recent marine deposits and available baseline information.

Contributed papers are now invited on various aspects of chemical contamination of the northwest Atlantic Ocean. The conference proceedings will be published after peer review.

For further information please contact the conference office: *Ocean Pollution 1981 Conference, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2. Telephone No. (902) 426-2479.*

Pollution des océans 1981

La Woods Hole Oceanographic Institution, du Massachusetts, et l'Institut d'océanographie Bedford, de Dartmouth (Nouvelle-Écosse), sont les co-parrains de cette conférence internationale qui traitera de la contamination chimique du nord-ouest de l'océan Atlantique. La conférence se tiendra du 19 au 23 octobre 1981 à l'Institut d'océanographie Bedford. Les organisateurs en sont Dr J. Farrington (Woods Hole Oceanographic Institution) et Dr J. H. Vandermeulen (Institut d'océanographie Bedford).

Les exposés qui y seront faits (sur invitation et sur proposition) traiteront de l'état du milieu marin dans le haute mer de l'Atlantique nord-ouest et des processus de sa contamination par les produits chimiques. La présence et la détection de substances chimiques étrangères (combustibles fossiles, hydrocarbures, produits organiques synthétiques, pesticides, métaux lourds) dans les sédiments, les eaux et les organismes des océans du monde constituent un problème qui doit être cerné. Les séances porteront sur les apports de contaminants et sur les processus qui régissent leurs déplacements ainsi que sur les problèmes auxquels on fait face lorsqu'il s'agit de les déceler. Il y aura aussi une séance spéciale au cours de laquelle des conférenciers invités parleront des radionucléides dans le milieu marin. Les sujets débattus seront les réservoirs de contaminants et les périodes de séjour, les concentrations et les écoulements et les interactions sédiments-eaux. On portera une attention particulière à la différentiation des contaminants et à la mobilité de ces derniers dans les dépôts marins récents et en fonction des informations fondamentales disponibles.

Nous invitons dès maintenant les personnes intéressées à proposer des exposés sur divers aspects de la contamination chimique du nord-ouest de l'océan Atlantique. Le compte rendu de la conférence sera publié après qu'il aura été revu par les pairs.

Pour obtenir de plus amples renseignements, on peut communiquer avec le bureau de la conférence à l'adresse suivante : *Conférence de 1981 sur la pollution des océans, Institut d'océanographie Bedford, Dartmouth (Nouvelle-Écosse) Canada B2Y 4A2. Téléphone: (902) 426-2479.*

Dynamics of Turbid Coastal Environments

This symposium will be held September 28 to October 2, 1981 at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada. It is organized and sponsored by the Department of Fisheries and Oceans Canada), the Canadian Atlantic Provinces Inter-University Committee on the Sciences, the Atlantic Research Laboratory of the National Research Council of Canada, and the Institute for Resource and Environmental Studies of Dalhousie University, Halifax, Nova Scotia.

The symposium participants will be examining recent research and multidisciplinary studies of dynamics in turbid coastal environments including physical oceanography, chemical oceanography, sedimentology, ecology, and fisheries. The common theme of all contributions will be the role, importance, and ramifications of heavy suspended sediment loads in coastal environments. Studies of the upper reaches of the Bay of Fundy in Canada, the Severn Estuary

Dynamique des eaux troubles côtières

Le colloque aura lieu du 28 septembre au 2 octobre 1981 à l'Institut océanographique de Bedford, Dartmouth (Nouvelle-Écosse), Canada. Il est organisé et parrainé par le ministère des Pêches et des Océans (Canada), le Comité interuniversitaire sur les sciences des provinces canadiennes de l'Atlantique, le laboratoire de recherches de l'Atlantique du Conseil national de recherches du Canada et l'Institut des études sur les ressources et l'environnement de l'Université Dalhousie, Halifax (Nouvelle-Écosse).

Les participants du colloque examineront les récents travaux de recherches et études multidisciplinaires dans le domaine de la dynamique des eaux troubles côtières, y compris en océanographie physique, en océanographie chimique, en sédimentologie, en écologie et dans le domaine des pêches. Le thème commun à toutes les contributions sera le rôle, l'importance et les ramifications des quantités de sédiments lourds en suspension dans les milieux côtiers.

in Great Britain, and the Wadden Sea in Europe, and others will be included.

The symposium will include approximately 36 papers, both invited and contributed, and the proceedings will be published after peer review.

For further information please contact: *Dr Donald C. Gordon Jr., Symposium Chairman, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2. Telephone No. (902) 426-3278.*

Y seront également incluses certaines études sur les parties supérieures de la baie de Fundy au Canada, l'estuaire de la Severn en Grande-Bretagne et sur la mer des Wadden en Europe, et autres.

Environ 36 communications seront présentées au colloque, tant par des invités qu'à titre de contribution, et le procès-verbal sera publié après révision par les pairs.

Pour renseignements, veuillez communiquer avec: *Dr Donald C. Gordon Jr., Président du colloque, Institut océanographique de Bedford, C.P. 1006, Dartmouth (Nouvelle-Écosse) B2Y 4A2. N^o de téléphone: (902) 426-3278.*

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Seasonal variation of potential nutrient limitation to chlorophyll production in southern Lake Huron **C. K. Lin and C. L. Schelske**

Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia **J.-G. J. Godin**

Morphological changes in gill epithelia of heat-stressed rainbow trout, *Salmo gairdneri*: evidence in support of a temperature-induced surface area change hypothesis **D. Jacobs, E. F. Osmond, E. L. Melisky, and C. H. Hocutt**

Effects of chronic zinc exposure on the growth, sexual maturity, reproduction, and bioaccumulation of the guppy, *Poecilia reticulata* **K. B. Pierson**

Genetic similarity among endemic Arctic char (*Salvelinus alpinus*) and implications for their management **I. Kornfield, K. F. Beland, J. R. Moring, and F. W. Kircheis**

Detecting temperature, fine structure, and mesoscale frontal regimes along line P in the northeastern Pacific Ocean **R. E. Thomson and L. S. C. Kuwahara**

Effect of boron on primary production of nanoplankton **D. V. Subba Rao**

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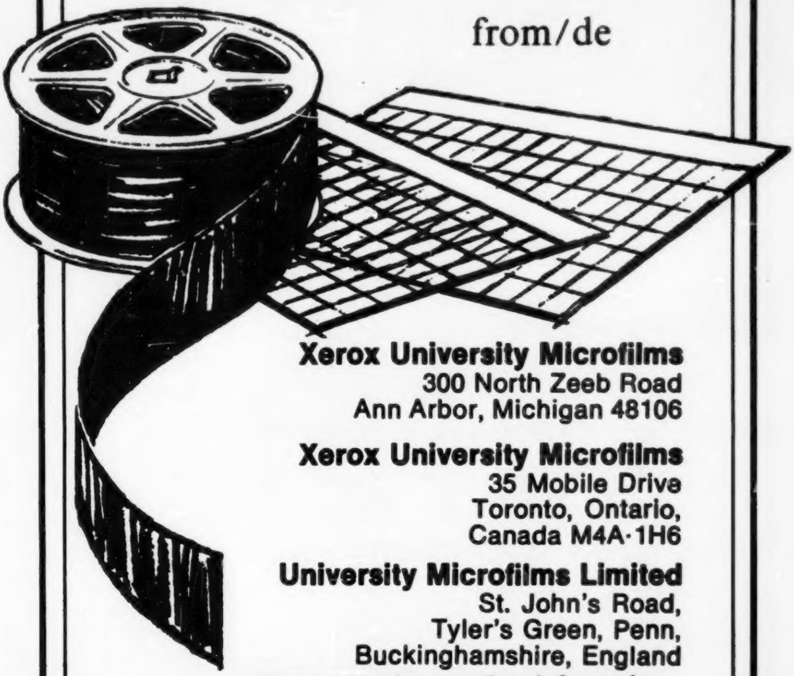

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